ESTUARINE ECOLOGY

Companion Website

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The website includes:

- All figures from the textbook as Power Point slides for downloading
- Supplementary text material for Chapter 17
- Chapters 1, 10, and 20

ESTUARINE ECOLOGY

Second Edition

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This book is dedicated to our students and to all others around the world who are interested in understanding, using, managing, and protecting estuarine ecosystems in a sustainable manner for future generations.

In memory of Dr. Scott W. Nixon for his important contributions to the field of estuarine ecology.

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PREFACE

This book is a textbook for a course in estuarine ecology designed to introduce students to the function and structure of estuarine ecosystems. It is designed primarily for an introductory graduate course, but it can also serve as a general resource book for estuarine ecologists. This book is the second edition of Estuarine Ecology; the first edition was published in 1989. Clearly there have been enormous advances since then, and this second edition has expanded from 13 to 21 chapters to cover these advances. Some topics, such as climate change, were of relatively minor interest prior to 1989, but have since become central to estuarine ecology. And there has been a dramatic increase in information about estuarine ecosystems, growing human impacts on these systems, and their value to society. This information is documented throughout the book. Another significant change is that we moved from a book in which most of the chapters were written by a small handful of authors to an edited volume with many authors. This was necessary because of the expansion of the bredth of estuarine science and the challenge of having a few authors adequately cover the subject. Thus, we reached out to a number of well-known experts to prepare individual chapters. But we endevoured to have them use a generally consistent format to ensure a comprehensive coverage of estuarine ecology.

The chapters in the book proceed logically through the science of estuarine ecology. The first chapter introduces estuaries and estuarine ecology, and describes some of the background, definitions, theory, and issues of estuarine ecology. The next two chapters deal with physical, geological, and chemical aspects of estuaries. The nature of estuarine ecosystems is to a great extent determined by a complex and dynamic physical, geological, and chemical environment. Therefore, a basic understanding of these topics is essential for a comprehension of estuarine ecology. Then there is a group of chapters on primary producers of estuaries. Two new chapters are added compared to the first edition so that phytoplankton, seagrasses, coastal marshes, mangroves, and benthic algae are covered. After that are two chapters on microbes in estuaries covering estuarine microbial ecology and estuarine microbial food webs, the latter being a new chapter for the second edition. Four chapters follow that covering estuarine consumers including zooplankton, benthos, nekton, and wildlife. The next three chapters cover emergent, holistic properties of estuarine ecosystems including metabolism, food webs, and budgets. All of these chapters develop detailed information on taxonomy, physiology, life histories, ecological role, growth, metabolism, and interaction with abiotic factors.

The last four chapters deal with fisheries, human impact and management, the effect of climate change on estuaries, and the role of modeling in estuarine science.

Our primary motivation for preparing this book was to update the first edition that is now very much out of date. In the intervening two decades since the publication of the first edition, many very good books have been written on estuarine science. But, we believe none of them really meets the need for an introductory text on estuarine ecology. Thus, we undertook this effort. We also hope that this book will become a "work in progress" that can be more easily updated on a regular basis because of the participation of many experts. The arduous task of preparing such a book by one or a few authors is part of the reason for the long delay in the second edition.

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INTRODUCTION TO ESTUARINE ECOLOGY

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1.1 BACKGROUND, THEORY, AND ISSUES

We begin this description of estuaries and their functions by defining estuaries very broadly as that portion of the earth's coastal zone where there is interaction of ocean water, fresh water, land, and atmosphere. Large estuarine zones are most common in low relief coastal regions such as the broad coastal plains of Europe and the east coast of North America. They are much less common in uplifted coastlines such as the Pacific edge of North and South America. We begin our assessment as broadly as possible to include all portions of the earth that interact at the edge of the sea because these regions influence the smaller scale ecosystems sometimes more narrowly defined as estuaries proper.

From the vantage point of an orbiting satellite, several of the most basic attributes of estuaries are observable. Plumes of sediment-laden water float seaward on the ocean surface from the largest rivers, such as the Amazon, the Ganges, and the Mississippi. Color differences among various water masses, representing waters of different histories and different biotic richness, are often apparent. Coastal waters in areas with significant riverine input and broad shelf areas generally appear more greenish brown than the

deep blue waters adjacent to many other coastlines. There are also atmospheric features of importance to estuaries obvious from space. Clouds commonly form directly over the edges of continents as one manifestation of the atmospheric ''thermal engine'' that maintains the freshwater cycle on which estuaries depend. At the altitude of a satellite, the dense human populations that proliferate in coastal zones are outlined at night by their lights.

The two most recent geological epochs, collectively named the Holocene, could be called *the age of the estuary*, for estuaries are abundant today, even though they are geologically tenuous. All present day estuaries are less than about 5000 years old, representing the time since sea level reached near its present level following the last ice age. Human populations flourished during this same period, in no small measure owing to exploitation of the rich estuarine resources of the coastal margin. Most ''cradles of civilization'' arose in deltaic and lower floodplain areas where natural biota was abundant and where flooding cycles produced the rich bottomland soils and readily available freshwater supplies on which agriculture flourished (Kennett and Kennett, 2006; Day et al., 2007). Early centers of civilization that developed in estuarine or deltaic environments include those of the Tabascan lowlands of Mexico; the valley of the Nile; Tigris-Euphrates, Yellow, and Indus

Rivers; and along the Andean coast of western South America where upwelling systems bordered estuarine systems.

Let us now continue our aerial survey of estuaries, but this time at a much lower altitude, about 1000 m, in a light airplane following the course of a coastal plain river in the temperate zone from its headwaters to the ocean. The headwater river is narrow with rapids and falls, but changes near the coast to a larger meandering form with broad marshy areas where the actual edge of the river is not always clearly evident. The color of the water changes from clear blue to yellowish brown as the river picks up silt. As the river water nears the coast tidal currents become apparent and, moving seaward, the influence of tidal currents becomes greater.

Along the banks of the estuary, fresh and brackish water marsh plants grow at the edges of embayments. These marshes are often flanked by rows of houses and yards and spanned by narrow piers to provide access to deeper water. Among these marshes, a variety of wading birds may be observed stalking their prey at the water's edge. Where the water is shallow and relatively clear, dark-colored patches indicate the presence of submersed grass beds.

As we travel seaward, the tidal influence becomes more important and the intertidal zone becomes more extensive. Larger piers and bulkheads interrupt the banks of the estuary, and brown mud flats come into view, as well as greenish gray oyster reefs fringing the banks or dotting the mud flats. Various birds such as oystercatchers feed on the reefs, along with an occasional raccoon. The mud flats are peppered with mud snails, and just beneath the surface are teeming communities of small worms and crustaceans. Various shore birds are feeding at the water's edge, and skimmers fly along in quiet areas, plowing a furrow in the water with their lower bill as they fish for silversides and other small fish. The darker colored path of a deep shipping channel maintained by dredging is evident toward the middle of the estuary and contrasts with the lighter colored shallows.

The mouth of the estuary takes the form of a broad sound that opens up behind a barrier island. The sound is shallow, and we can see porpoises herding schools of juvenile menhaden, followed by gulls trying to get in on the action. Crab pot buoys and fishing boats are much in evidence. On either side of the barrier island are narrow passes with visible eddies and strange wave patterns, indicating rapid and complex currents.

Along the ocean beach, a number of shrimp boats raise long spiraling muddy plumes of sediment as they drag their trawls along the bottom. A kilometer or so offshore of the tidal passes the water changes color from dark brownish green to a lighter, less turbid green. Further offshore, it is a darker and bluer color.

On the landward side of most such barrier islands, there are flat intertidal areas colonized by salt marsh plants. The highest part of the island includes some oak trees. The beach may include a series of dunes, with the farthest from the ocean being covered with vegetation and the nearer dunes being less vegetated. The seaward side of the dune closest to the ocean has much less vegetation because the wave energy from storms makes it difficult for plants to survive. In parts of the beach–barrier system, vacation houses have replaced the dunes, and straight navigation channels have replaced twisting tidal channels.

In summary, from many elevations estuaries can be seen as complex, dynamic, and biotically rich environments dominated by physical forces and impacted by human activity. Their study requires a consideration and knowledge of geology, hydrology, chemistry, physics, and biology. Ideally, we can integrate knowledge gained through these specific disciplines using what we call systems science. This book is an introduction to the specifics of estuarine science and their integration into a coherent view of estuaries as ecosystems. We show how estuaries are different from one another and how they are similar, and why we need to preserve them while enhancing their value to society.

We will begin by describing a very generalized estuary, to provide the reader with an introduction to the geology, physics, chemistry, and biology of estuaries. This is done with a certain danger because, as the rest of the book shows, estuaries are characterized as much by differences as by similarities. Nevertheless, in this chapter, we attempt to describe a generalized estuary. But before we proceed further, we will define an estuary.

1.2 DEFINITIONS, TERMS, AND OBJECTIVES

1.2.1 Definitions of Estuary and of Ecology and Difficulties in Applying These Definitions to Real Estuaries

The term *estuary* comes from the Latin *aestus* meaning heat, boiling, or tide. Specifically, the adjective *asetuarium* means tidal. Thus, the *Oxford Dictionary* defines estuary as ''the tidal mouth of a great river, where the tide meets the current.'' *Webster's Dictionary* is

more specific: ''(a) a passage, as the mouth of a river or lake where the tide meets the river current; more commonly, an arm of the sea at the lower end of a river; a firth. (b) In physical geography, a drowned river mouth, caused by the sinking of land near the coast.''

Perhaps the most widely quoted definition of an estuary in the scientific literature is given by Pritchard (1967): ''An estuary is a semienclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage.'' Certainly, one of the most characteristic attributes of most coastal areas is the action of the tide. Pritchard's definition makes no specific mention of tide, although the mixing of seawater and fresh water implies this. There are, however, many nontidal or minimally tidal seas, such as the Mediterranean Sea and the Black Sea, where fresh and salt water mix.

There are also estuaries in semiarid regions that may not receive any fresh water for long periods; sometimes, as in the Pacific coast of California and Mexico, Western Australia, and several parts of Africa, the estuary may become blocked by longshore sand drift, so that it is ephemerally isolated from the sea for months to even years. In other regions, the tidal limit, sometimes with a tidal bore, may reach 100 km or more above the limits of salt water intrusion. So Pritchard's definition of estuary excludes some coastal areas where estuarine ecology is studied today.

In an attempt to address the limitations of Pritchard's definition, Fairbridge (1980) gave a more comprehensive definition of an estuary: An estuary is an inlet of the sea reaching into a river valley as far as the upper limit of tidal rise, usually being divisible into three sectors: (i) a marine or lower estuary, in free connection with the open sea; (ii) a middle estuary subject to strong salt and fresh water mixing; and (iii) an upper or fluvial estuary, characterized by fresh water but subject to daily tidal action. The limits between these sectors are variable and subject to constant changes in the river discharge.

Fairbridge's definition excludes some coastal geomorphic features such as lagoons, deltas, and sounds and also nontidal estuaries. The distinctions among these different terms are treated in detail in Chapter 2, but characteristic estuarine ecosystems have developed in all these coastal systems. Therefore, when the terms *estuary* and *estuarine* are used in this book, unless specifically stated otherwise, they are meant in a general ecological sense rather than any specific narrower geological sense. Valle-Levinson (2010) provides an overview of definitions and classifications of estuaries.

All of the definitions of estuaries given above reflect, for the most part, physical and geological characteristics of estuaries. But why is this so? The people who first defined and classified estuaries were geologists and physical oceanographers, because in many respects the most salient features of estuaries are physical and geomorphic. And the ecosystems that exist in estuaries are often physically dominated. We can illustrate this point by comparing an estuarine ecosystem with a tropical forest ecosystem. A visitor to a rain forest is immediately struck by the richness of the vegetation. If the visitor stays in the forest for some time, he or she will notice that it rains a lot and the temperature is warm. If the visitor is a careful observer, he or she will perhaps learn about the soils of the forest. But the most striking characteristic is the vegetation. Rain forests are biologically dominated systems and have been described primarily by their biological characteristics.

In contrast, a visitor to an estuary cannot escape noticing the impact of abiotic characteristics. These include the rise and fall of the tide, complex water movements, high turbidity levels, and different salt concentrations. The nature of land-forms such as beaches, barrier islands, mud flats, and deltas and the geometry of the basin are also very noticeable. There are, of course, outstanding biotic characteristics of estuaries such as salt marshes, mangrove swamps, submersed grass beds, and oyster reefs. But, in general, one has to look carefully to obtain even an idea of the biological structure of estuaries.

The visibility of the abiotic attributes of estuaries reflects the fact that estuaries are, to a large degree, physically dominated ecosystems. To begin to understand estuarine ecosystems and how they functions, an estuarine ecologist must have a good understanding of the geology, physical oceanography, and chemistry of estuaries. Thus, one of the basic goals of Chapters 2 and 3 is to provide physical and chemical bases that will lead to an understanding of the biotic processes.

Before we go further, it is necessary to define ecology, since this book is about estuarine ecology. Usually ecology is defined as the study of the relation of organisms or groups of organisms to each other and to their environment. Margalef (1968) gives a definition of ecology that is, perhaps, more appropriate to the way we approach estuarine ecology. He stated that ''ecology is the study of systems at the level in which individuals or whole organisms can be considered as elements of interaction, either among

themselves, or with a loosely organized environmental matrix. Systems at this level are called *ecosystems*, and ecology is the biology of ecosystems.'' Thus, in this book, we will consider the environmental matrix of estuaries, the interactions among specific organisms and the environment, and the structure and functioning of whole estuarine ecosystems.

1.3 FIVE VIEWS OF A GENERALIZED ESTUARY

We now discuss estuaries in a more systematic and scientific manner, and we do this through five views of a generalized estuary, emphasizing common characteristics among these divergent systems.

1.3.1 Top View

The first view of a generalized estuary is from above (Fig. 1.1). At one end there is a river entering a large bay and at the other end a barrier island separating the bay from the ocean. Wave energy along the barrier island is high and there is a wide sandy beach. On the beach, there is little immediate evidence of life other than a few birds. Studies have shown, however, that abundant and diverse communities of tiny organisms live among the sand grains on beaches. Wave energy is very important to these organisms because the waves pump water containing oxygen and food constantly through the sand while carrying away waste products. The beach is an area of very high physical energy and the sediments

are completely oxidized. This is an example of the importance of physical processes in determining the biotic characteristics of the estuarine environment.

In the tidal pass, the water is still clear and the salinity high. Wave activity is somewhat reduced but currents are still strong. At the entrance to the pass, the sediments are still sandy and completely oxidized, but are beyond the influence of strong currents, anoxic conditions occur a few tens of centimeters below the sediment surface. The biota is abundant and diverse in the pass, including epifauna, in contrast to the barren surface of the beach. The pass is often the deepest part of the estuary.

As we move through the estuary, there are distinct changes in depth, physical energy levels (current and turbulence), water clarity, salinity, biota, chemical concentrations, oxidizing and anoxic conditions in the sediments, and so on. In intertidal and subtidal areas with significant currents, there are often worm flats or mollusk beds. These filter-feeding organisms depend on currents to transport oxygen and food and to carry away wastes.

In the shallow subtidal waters of somewhat reduced currents where light reaches the bottom, marine meadows of submersed aquatic vegetation or seagrass beds often occur. Water clarity is high and sediments are finer, partially as a result of the grass's ability to trap sediments. The reduced zone of the sediments extends to within a centimeter or less of the surface. In high salinity tropical waters, these submersed grass beds are often dominated by turtle grass, *Thalassia testudinum* and in the temperate zone by eel grass, *Zostera marina*. In lower salinity waters
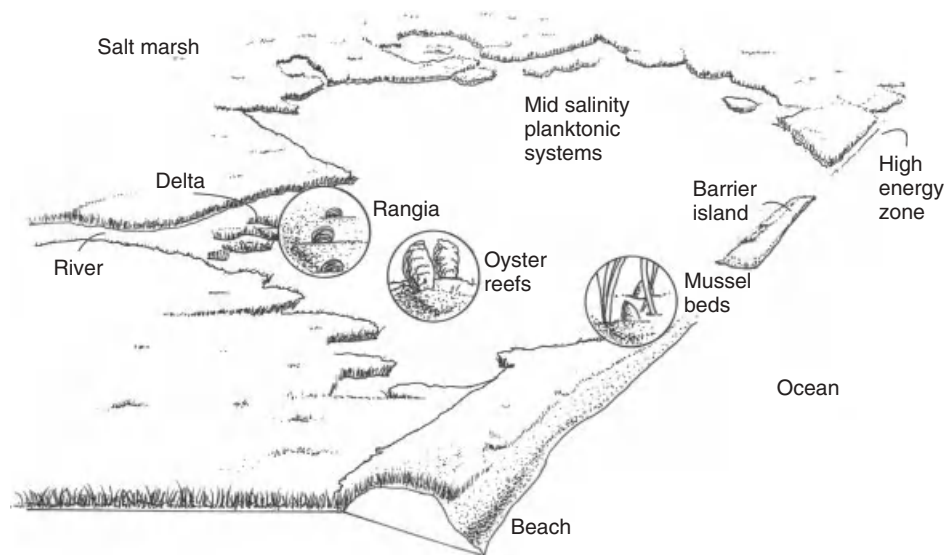
FIGURE 1.1 Idealized oblique aerial view of a typical estuarine system showing some of the major subsystems.

(<5 ppt) genera such as *Ruppia, Potamogeton*, and *Valisneria* are common.

In this typical estuary, salinity decreases steadily from the ocean to the river. The high salinity area of the estuary (30–35 ppt), is called *polyhaline*, middle salinities around 15 ppt constitute the *mesohaline*, and the low salinity region (0–5 ppt) is called the *oligohaline zone*.

Bordering the estuary in areas of mild to sluggish currents are intertidal wetlands where salt marshes occur in the temperate zone and mangrove swamps occur in the tropics. These are areas of turbid waters and highly reducing and very fine sediments. The vegetation has very high growth rates and the animals tend to be deposit feeders.

1.3.2 Cross-Section View

A cross-section view of the estuary (Fig. 1.2) illustrates a number of vertical as well as horizontal attributes of estuarine ecosystems. Vertical gradients are important in determining the nature of these ecosystems. Perhaps the most obvious is the intertidal zone that is alternately flooded and exposed. In the intertidal zone, there may be salt marsh or mangrove wetlands, algal beds, sand or mud flats, or reefs of oysters, mussels, or clams. Most organisms that live in the intertidal zone have developed special adaptations, which are discussed in numerous places in this book and specifically in chapters 6, 7, and 12.

A second important vertical gradient is that of light. The lighted zone in an aquatic system is called the *euphotic* zone, while the zone with no light is the *aphotic* zone. Obviously, photosynthesis occurs only in the euphotic zone. Where light reaches the bottom, plants can live attached to the bottom. Estuarine water clarity tends to be much greater near the ocean, so both rooted plants and plankton can generally photosynthesize at greater depths than in lower salinity regions. Animals that live in the aphotic zone are dependent on food being transported from other parts of the estuary.

Another extremely important gradient for biological and chemical processes in estuaries is that from oxidizing (where oxygen is present) to reducing (where oxygen is absent) conditions. An oxidizing environment is also called *aerobic* or *oxic* and a reducing one *anaerobic* or *anoxic*. The estuarine water column is normally aerobic, but estuarine sediments usually are anaerobic a short distance below the sediment surface. The amount of oxygen in the sediments is related both to the rate at which oxygen moves into the sediments and the rate at which it is consumed by the metabolic activity of microbes. In areas with high physical energies, such as waves or strong currents, there are well-sorted coarse sediments that are oxidized. The physical energy serves both to replenish the oxygen to the sediments and to wash out finer materials that, for several reasons, support microbial communities that consume oxygen rapidly. The opposite condition exists in areas of fine sediments. There the currents are too weak to sort the sediments or replenish oxygen rapidly, and in some cases (such as highly reduced marsh soils), anaerobic conditions extend up to the sediment surface. Since most estuaries are underlain with fine sediments, the reduced zone is widespread.

The activities of the biota, including the construction of burrows by organisms such as worms and fiddler crabs, facilitate the movement of water and oxygen through sediments. Many plants that grow in
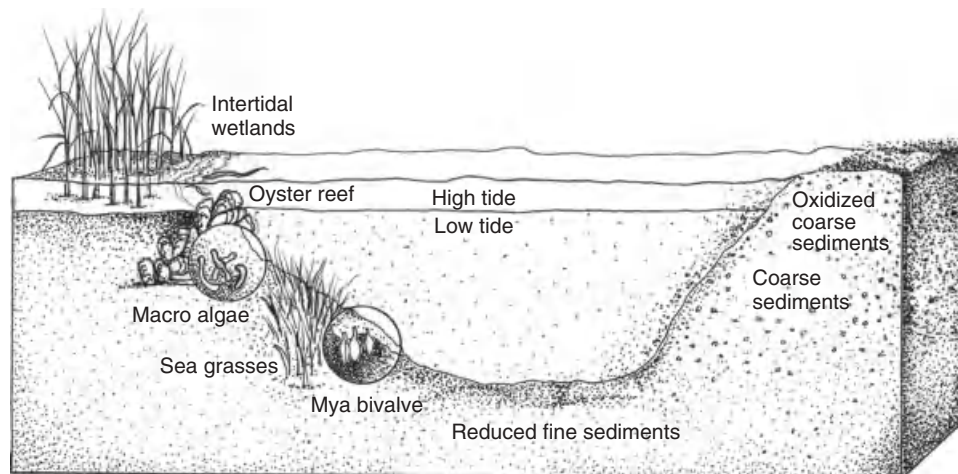
FIGURE 1.2   Idealized cross section through a typical estuary showing vertical distribution of several important elements; note that organism sizes and vertical scale are exaggerated.

reduced conditions, including species of the genera *Spartina*, actively pump oxygen into the soil and create a thin oxidized zone around their roots and support an aerobic root-associated microbial community.

1.3.3 Longitudinal Section

The longitudinal section (Fig. 1.3) demonstrates some of the attributes that result from the mixing of fresh water and seawater. Salinity gradually increases along the length of estuaries, and the isohalines (lines of equal salinity) show that salinity generally increases with depth. This salinity distribution results from the density difference between salt and fresh water. Fresh water from the river tends to flow on top of the salt water because it is less dense. As the fresh water flows to the sea, deeper salt water mixes with it, making it saltier. This outward flow of fresher water causes more salt water to move into the estuary and results in a net outflow of fresh water to the sea at the surface and a net inflow of salt water on the bottom. This circulation pattern, and the resulting salinity distribution, is a general feature of many estuaries that have significant river input and is discussed in more detail in Chapter 2.

We again see the euphotic and aphotic zones in the longitudinal section, but the depth of the euphotic zone decreases toward fresh water because of increasing turbidity. The most turbid water occurs at salinities from 1 to 5 ppt, and this "turbidity maximum" is a result of several physical and chemical changes that occur as river water and sea water mix. These changes are addressed in Chapter 3.

Because this transect is through the deepest part of the estuary, there are fine sediments and reducing conditions below the sediment surface along the entire transect. At the mouth of the river, the "platform" of riverine sediments that have settled out of the water where the river enters the estuarine bay is to be noted.

Organisms that occur in the water column include bacteria, phytoplankton, zooplankton, and nekton (freely swimming organisms such as fishes). The sizes of these organisms range from bacteria that are $<1\,\mu m$ to large animals such as seals and dolphins. Benthic animals include infauna that live in the sediments such as polychaete worms, amphipods, and the very small meiofauna. Of special note is the dense bed of the clam *Rangia cuneata* in the oligohaline region. The diversity of benthic organisms along this transect is discussed in more detail later in this chapter as well as in Chapter 12 on estuarine benthos.

1.3.4 A Typical Estuarine Food Web

Thus far our observations of the typical estuary have been of the structure and, as such, have been rather static. We now discuss more dynamic aspects of the estuary by considering a typical estuarine food web (Fig. 1.4). This allows for a more detailed consideration of some of the organisms that live in estuaries. For illustrative purposes, we compare estuarine and marine systems.

We begin by listing several terms with definitions derived from E.P. Odum 1971. The transfer of food energy from the source in plants (or more appropriately, primary producers) through a series of organisms eating one another is referred to as a *food chain* or, more properly, *food web*, for food chains interconnect with one another. The word *trophic* is used interchangably with food, and trophic dynamics refers to the pattern of food production and consumption as it occurs and changes over time.
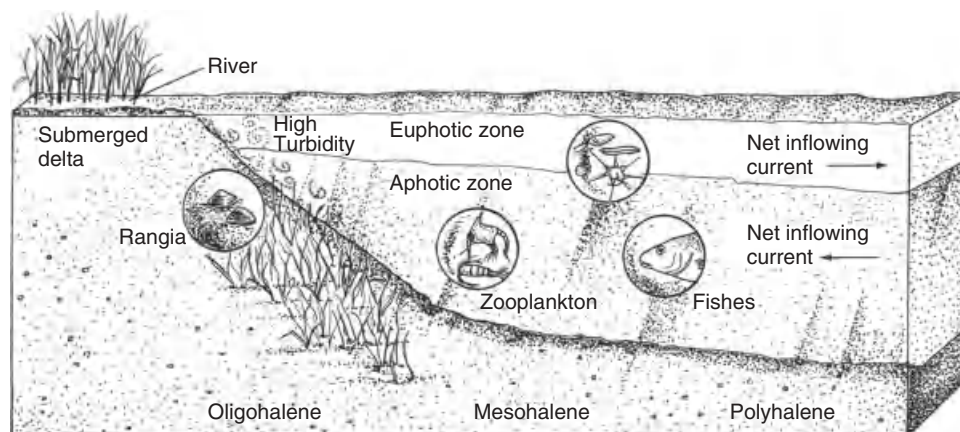
FIGURE 1.3 Idealized longitudinal section through a typical estuary from river to the sea. The vertical scale is exaggerated, and the darker area near the sediment surface indicates an oxidized zone.

The trophic dynamics of estuaries tend to be complex. Figure 1.4 illustrates a number of important characteristics of estuarine trophic dynamics. First, there are almost always several different types of primary producers in estuaries, including phytoplankton, salt marsh plants, mangroves, submersed sea grasses, and benthic algae. In contrast, the open ocean has only phytoplankton. There are other important distinctions between the open sea and estuaries. For example, in the sea, practically all phytoplankton are consumed alive. A food web that begins with consumption of live plants is called a *grazing food web*. In estuaries, many important plants are not heavily grazed, but die and begin to decompose before being consumed. This decomposing material is called *organic detritus* and the food web it supports is called a *detrital food web*. Organic detritus is an important food in estuaries, and an important area of research over the past four decades concerns detrital dynamics. Detritus is considered in a number of chapters, especially Chapters 9 and 16 on microbial ecology and trophic webs.

Nevertheless, the part of the estuarine food web that is the most readily recognizable to students is the grazing web based on phytoplankton. These small primary producers are eaten by zooplankton, which are then eaten by small planktivorous fish. In this example, they are herring, but in other estuaries, these fish may be anchovies or sardines. Zooplankton are also eaten by larvae of larger fish. At the top of the food web are larger carnivores such as bluefish. We now know that phytoplankton and the organisms that consume them form an extremely complex set of interactions called the *microbial food web*. This is covered in Chapters 10 and 11.

An extremely important characteristic of estuarine food webs is the importance of the bottom of estuaries. First, a variety of plants grow on the bottom in shallow waters (e.g., marsh grasses, sea grasses, and benthic algae). Second, there is significant flow of food and inorganic nutrients from the water column to the bottom as well as in the opposite direction. Benthic animals such as oysters, clams, and mussels are filter feeders; that is, they remain in one place and concentrate food that flows past them in the water currents. There are other benthic organisms that live in areas of weak currents. They move over and through the sediments and take food from the sediment itself. These are called *deposit feeders* and include worms, amphipods, and a host of other small organisms. There are also a large number of non-bottom-dwelling organisms that feed on the bottom. These include a variety of invertebrates, fish, and birds. In fact, the majority of fish species found in estuaries have adaptations for bottom feeding.

All of this flow of food energy from phytoplankton, detritus, and through the bottom converges on a group of top carnivores that are generalist feeders on a wide variety of organisms. These top carnivores include many species of fish, including sea trout, striped bass, and flounder, birds such as sea gulls, and mammals such as seals and dolphins.

In summary, estuarine trophic dynamics are characterized by a variety of primary producers; grazing
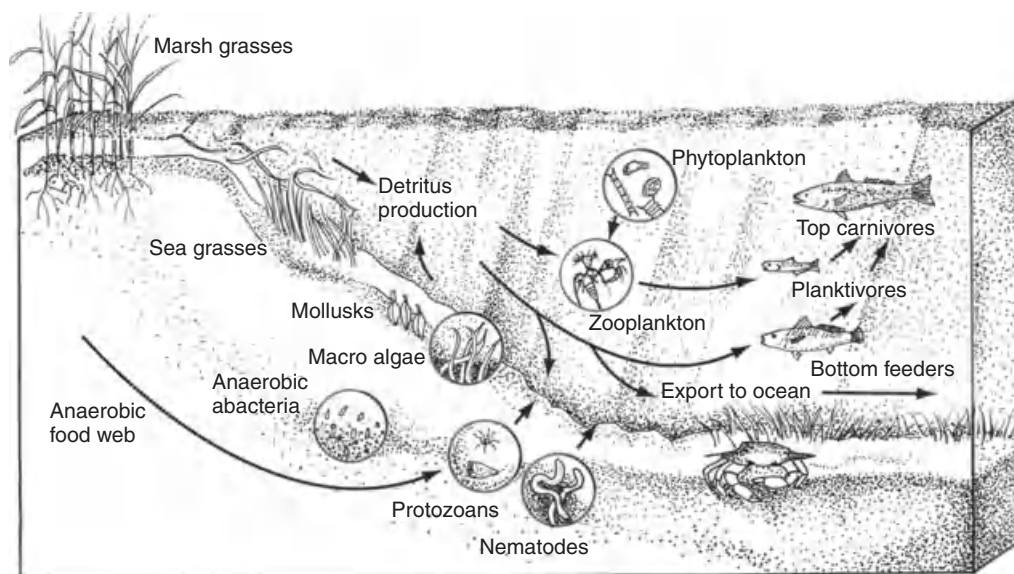
FIGURE 1.4 Food web diagram for a typical estuarine ecosystem showing some feeding links among some of the major trophic groupings. Black lines and arrows indicate flow of food from source to consumer.

and detrital food chains; a high degree of inter-action between the water column and bottom; a complex, highly interconnected food web; and a large number of generalist feeders. More details on food webs is found throughout the book and especially in Chapter 16.

1.3.5 An Estuarine Energy-Flow Diagram

Thus far, we have discussed visible aspects of estuarine ecosystems. We can see an oyster reef and a salt marsh and a sample taken from the bottom. We can watch a trout eat an anchovy and, if we have a microscope, we can even observe a zooplankter ingesting a phytoplankton cell. But important processes go on which are not visible. We cannot see sunlight interacting with chemicals during photosynthesis. Nor can we watch phosphorus flowing out of bottom sediments and being moved into surface waters by currents. It is very difficult to measure organic detritus flowing out of a marsh, much less visibly observe it being degraded and consumed by bacteria. Nevertheless, an understanding of these and other processes is essential if we are to begin to comprehend how estuaries work. Thus, in this section, we use an energy-flow diagram (Fig. 1.5), both to present systematically some of the concepts we have discussed and to conceptualize some of these invisible processes. To do this, we use the symbols developed by H.T. Odum (1971, 1983).

The diagram illustrates the grazing and detrital food webs we discussed in the previous section. It shows the importance of tidal currents in transporting detritus out of the marsh and in moving phytoplankton to benthic filter feeders. The dynamics of nutrient cycling are important and complex in estuaries. Our diagram shows input of nutrients and
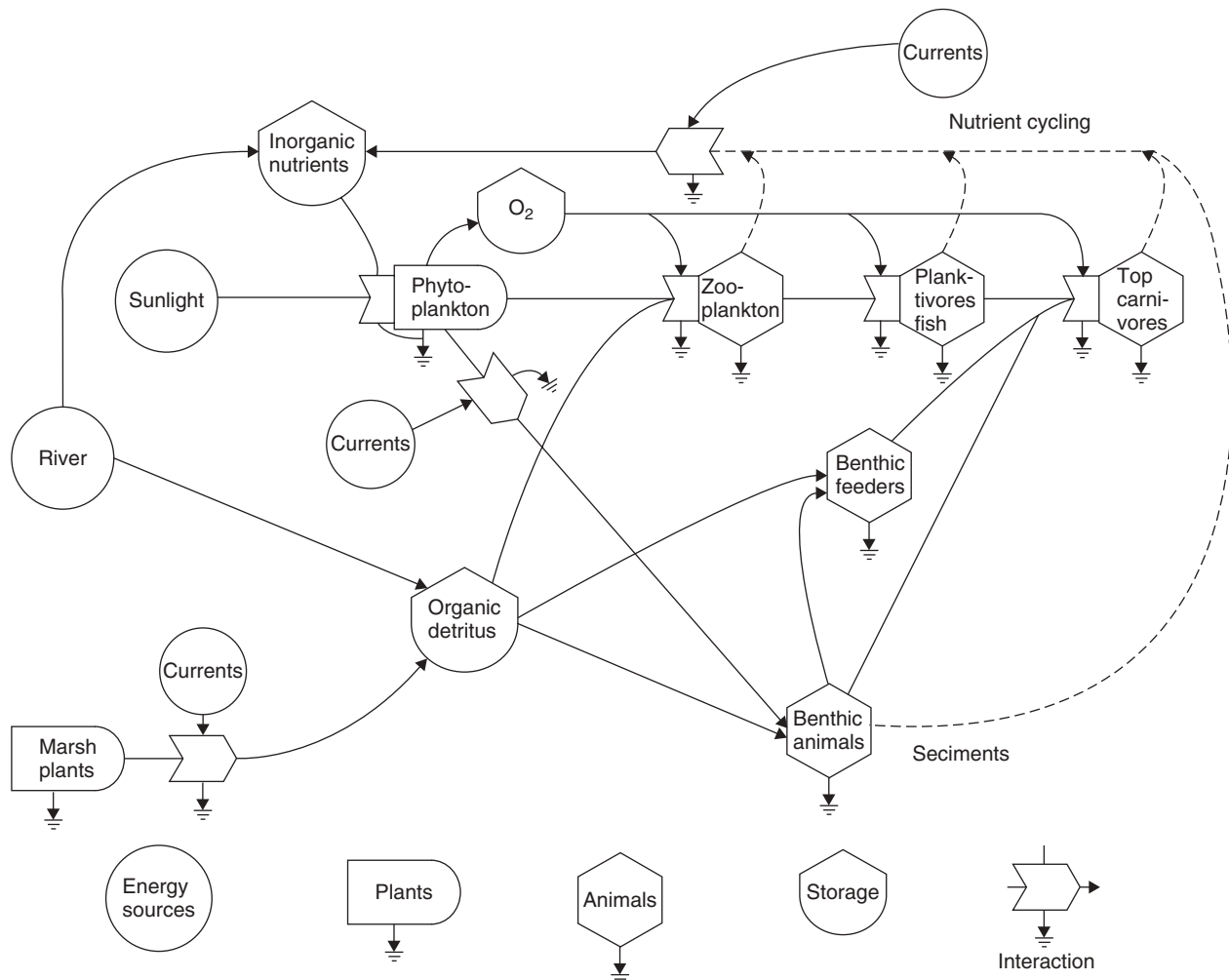
FIGURE 1.5   An energy-flow diagram illustrating some major structural and functional attributes of estuarine ecosystems. Note that the five types (shapes) of symbols used are defined along the bottom of the figure.

organic matter from the river as well as recycling from both sediment and water-column organisms. Again, the importance of currents in transporting nutrients is illustrated. Finally, the diagram shows that there is an interaction of sunlight and inorganic nutrients during primary production by phytoplankton and that plankton produce oxygen that is subsequently used by animals. There are, of course, many interactions and details left out of this energy diagram as well as the preceding views of estuaries. Throughout this book, the concepts we have introduced here are developed in much more detail to provide a fuller general understanding of estuaries. At this point, however, the reader should have a good foundation to begin a more in-depth study of estuaries. In the following section, we discuss a classification of estuarine ecosystems.

1.4 ESTUARINE HABITAT TYPES

The previous two sections demonstrated the high diversity of habitat types within estuarine systems. This diversity is caused by two things. First, from an abiotic point of view, estuaries include a great number of physical habitats, including beaches, passes, intertidal and shallow subtidal flats, deeper areas, and deltas. Second, adapted assemblages of organisms can fully exploit each of these different habitats and, in many cases, can dramatically alter those habitats, further expanding the total habitat diversity of estuaries. For example, in the intertidal zone, there may be salt marshes, tide pools, algal flats, mud flats, oyster reefs, and mussel beds. Oyster reefs and mussel beds, in turn, create new types of habitat by changing the physical environment. Subtidal areas can include seagrass beds, sandy shoals, soft muddy bottoms, or mollusk beds. Some of the more important biotic habitats are described in Table 1.1.

1.4.1 Characterization of the Ecosystem

We defined estuary and ecology, but because these definitions are so broad, it is difficult to define "estuarine ecosystems," except as those ecosystems that have developed and persist in estuaries. We can easily describe, however, the abiotic factors that are most important in determining the specific nature of estuarine ecosystems as well as the salient ecological characteristics of these ecosystems.

The physical environment (climate, geomorphology, presence or absence of water, salt, etc.) is the primary determinant of the type of ecosystem that will develop in a particular location. The constancy and regularity, or the lack thereof, of the physical environment is an important attribute of physical conditions that influence the biota. That is, the biota is more determined by the degree of change over various time intervals (e.g., diel, tidal, and seasonal), than by the absolute level of such factors as microclimate, water movement, chemical cycling, and physical structure. Both abiotic factors and the biota itself can reduce the degree of these fluctuations. Tropical rain forests and coral reefs are examples of ecosystems where the ambient physical environment is greatly modified by the biota. In contrast, alpine lichen herb and sandy beach ecosystems are strongly affected by physical inputs and are relatively unaffected by the biota. Estuarine ecosystems are intermediate between these extremes but are still strongly physically dominated.

The following abiotic features are important in determining the specific nature of estuaries:

1. The degree to which they are protected from and hence buffered against direct oceanic forces.
2. The quantity of fresh water input along with the amount of associated dissolved and suspended materials.
3. The water circulation patterns as determined by riverine and tidal currents, winds, and geomorphology. Tides are particularly important because they exert a profound influence on estuarine circulation and biological processes.
4. The depth of the estuary. Where estuaries are shallow there is a stronger interaction between the water column and the bottom. This allows, for example, nutrients released from the bottom to be used by phytoplankton in the surface waters.
5. The sharpness and pattern of the gradient in salinity from the sea to fresh water. This salinity variation has a pronounced impact on water circulation as well as on many biological processes and organisms.
6. The rate of geomorphological change is rapid compared to that in many terrestrial systems. Sand banks and mud flats form, degrade, and migrate within estuaries. Wetlands form at the mouths of rivers as sediments are deposited. Biogenic processes, such as reef formation, contribute to the geomorphology of estuaries.

Most estuarine ecosystems are open, variable systems dominated and subsidized by physical processes, resulting in large exchanges of biotic and nonbiotic materials, including water, salt, nutrients, sediments, and organisms, with neighboring systems. The exchange of organisms over millions of years has

TABLE 1.1 Key physical and biological characteristics of eight common estuarine habitats

Habitat	Physical Characteristics	Biological Characteristics
High physical energy	Tidal passes and beaches; strong currents and or waves; often clean water; coarse sediments such as sand; well-oxidized water column and sediments; generally high salinities	Benthos dominated by filter feeders; high diversity and biomass; high rates of metabolism supported by current transport of food; heterotrophic; motile organisms mostly transient
Mid-estuarine systems: middle-salinity plankton-nekton system	Strong to moderate turbulence (waves and currents); salinity 10–25 ppt; oxygenated water column; bottom deeper than euphotic zone; medium water clarity	Grazing food chain of phytoplankton, zooplankton, fishes; diatoms, dinoflagellates, and nanoplankton; common phytoplankters; copepods and meroplankton important zooplankters; relatively high rates of primary production with strong seasonal pulse in temperate zone disappearing in the tropical, balanced community metabolism; intermediate diversity
Mid-estuarine systems: deep benthos	Sluggish currents; fine sediments; no light on bottom; reducing conditions just below sediment surface; water column normally oxygenated	Deposit feeders dominate (worms and amphipods); low density and biomass; heterotrophic with relatively low metabolic rate; low diversity
Shallow littoral areas: submerged grass beds	Moderate to strong currents; bottom within euphotic zone; oxygenated water column; sediment reduced just below surface; sediments range from sandy to fine	High salinity grass beds dominated by eel grass (*Zostera*) in temperate zone and by turtle grass (*Thalassia*) in tropics; high rates of gross primary productivity, community net productive; detrital food chain important; direct grazing increases in tropics; both deposit feeders and filter feeders important in benthos; high biomass, low diversity; complex chemical cycling; important nursery and feeding area for migratory species; high epiphytic community
Shallow littoral areas: algal mats	Shallow, clear, often hypersaline water; sediments sandy to fine silts: highly reduced below mat; large oxygen changes due to metabolic activity	Blue-green algal mats; extremely productive, P/R close to one; low consumer diversity
Wetlands	Sluggish currents; intertidal wetlands act as sediment traps, sediments generally very soft often with peats; strong reducing conditions in sediments sometimes to sediment surface; often low oxygen in water column; complex chemical cycling; wetlands occur from fresh to marine salinities and from the arctic to the tropics	Saline wetlands characterized by marshes (*Spartina*) in temperate zones and mangrove swamps (*Rhizophora*) in tropics; freshwater wetlands swamp or marsh; freshwater areas have high producer diversity; high rates of gross primary production; detrital food chain important; high biomass of both producers and consumers; low diversity; deposit feeders most common; important nursery and feeding area for migratory species
Reefs, worm, and clam flats	More or less constant currents—moderate to strong; intertidal or subtidal; oxygenated water column; reduced sediments; reef structure often amplifies currents; intermediate salinities for oysters; sediments for mollusks flats normally oxygenated; oyster reefs normally in fine, soft sediments, others in firmer sediments of sand or shell	High biomass; low diversity; relatively high food supplies in water column; filter feeders predominate; high rates of metabolism; heterotrophic; often exploited commercially; *Crassostrea* and *Ostrea* common genera of oysters; oysters epifaunal, flats populated by infauna organisms
Oligohaline	Located at river mouth–estuary boundary; highly variable salinity; water contains high levels of suspended solids and nutrients; high sedimentation rates, high turbidity, "nutrient trap"	Low species diversity; very high biomass; high rates of metabolism; heterotrophic; filter feeders dominate; *Rangea cuneata* and *Mya arenaria* very common in south and north temperate, respectively; heavily used by migratory fishes

resulted in a rich genetic heritage, and the biota is derived from marine, freshwater, and terrestrial sources. Over time periods of hundreds to thousands of years, deltas grow and erode and barrier islands shift. On shorter timescales, salinity changes with tide and river flow, and water levels fluctuate so that the intertidal region is subjected to wetting and drying and extremes of temperature. But estuarine organisms have developed physiological and behavioral patterns to deal with this dynamic environment, and many are able to directly modify the physical environment. Many organisms use the intense and variable physical energies as subsidies, as, for example, in the case of an oyster reef ''using'' the flow of tides to exploit phytoplankton produced elsewhere. Nevertheless, such an ever-changing world imposes considerable potential stress on estuarine organisms because large changes in salinity, temperature, and so on, can be deleterious, even lethal, for estuarine organisms. The relative importance of physical forces as subsidies or stresses forms the basis for the estuarine classification discussed in the following section.

1.4.2 Functional Classifications of Estuarine Ecosystems

Chapter 2 presents several estuarine classification schemes based on physical and geomorphic characteristics. These definitions help us understand the origin and physical nature of estuaries and can be used as the beginnings of an estuarine classification system. From the standpoint of estuarine ecology, however, we need a classification system that leads to a better understanding of estuaries as ecosystems. We discuss here an approach to conceptualize estuaries based on energy inputs and landscape features.

Odum and Copeland (1972) proposed a ''functional'' system for understanding and classifying coastal ecosystems based on an analysis of energetics. We like their approach because it is a true ecosystem classification addressing both biotic and abiotic properties and it recognizes the importance of energy. Their idea is that the status of an ecosystem is a balance between energies that build structure and order and stresses that cause a loss of structure and order. The former are called *energy sources* or *ordering energies* and the latter *energy stresses* or *disordering energies*. This idea is shown diagrammatically in Figure 1.6a.

We want to emphasize that energy sources and stresses are not always mutually exclusive categories of energies, but rather that a particular energetic force affects organisms relative to the ecosystem (or part of an ecosystem) in question. A few examples illustrate this point. Moving water can be either an energy source or stress in estuarine ecosystems. Moderate currents are a source of energy for seagrass beds because they transport organic matter and nutrients to the beds and wastes away. If the currents become very strong with high waves, however, the grass bed may be eroded. In the latter case, the hydraulic energy is a stress. But the same strong waves are an energy source for tiny animals living among the sand grains on a beach because the waves pump oxygen and food through the sand. Likewise, heat from the sun is an energy source for a marsh because it increases the rate of metabolism. But the intense heat of a fire will destroy a marsh.

The distinction between energy source and energy stress is the central concept in this classification system. Whether an energy input is ordering or disordering depends on the particular system or subsystem in consideration, and it is the balance between the two that is important. If energy sources are greater than stresses, the system will build structure and maintain order. However, if stresses are greater, there will be a loss of structure and order.

There are three general categories of energy sources for estuarine ecosystems: (i) the mechanical energy of moving water, (ii) sunlight, and (iii) organic and inorganic fuels imported into estuaries (Fig. 1.6b). Moving water does work, such as by connecting trophic components in the bottom and surface waters, bringing food to filter feeders, recycling nutrients, and removing wastes. Organisms in effect ''conserve'' their own energy by using the water current energy instead. The energy of sunlight drives photosynthesis of plants, which in turn supports estuarine food chains. Sun energy also supplies heat and thus produces thermal gradients in estuarine ecosystems. Supplementary organic and inorganic fuels are imported into estuaries via rivers, terrestrial runoff, and the sea. The organic matter is an added food to that produced in estuaries and the inorganic compounds such as nitrogen can increase photosynthesis by providing needed materials.

There are three general categories of stress energies for estuarine ecosystems: (i) stress due to energy diverted from the system, (ii) stress due to microscale random disordering, and (iii) stress due to forced losses within the system (Fig. 1.6c). Stress caused by energy diverted refers to energy that could be a source but is, for some reason, lost. For example, turbidity caused by natural conditions or human activities lowers the amount of light energy that enters the water column and thus the photosynthesis of deeper submersed plants. For another, when a marsh is impounded, the energy of tidal currents is
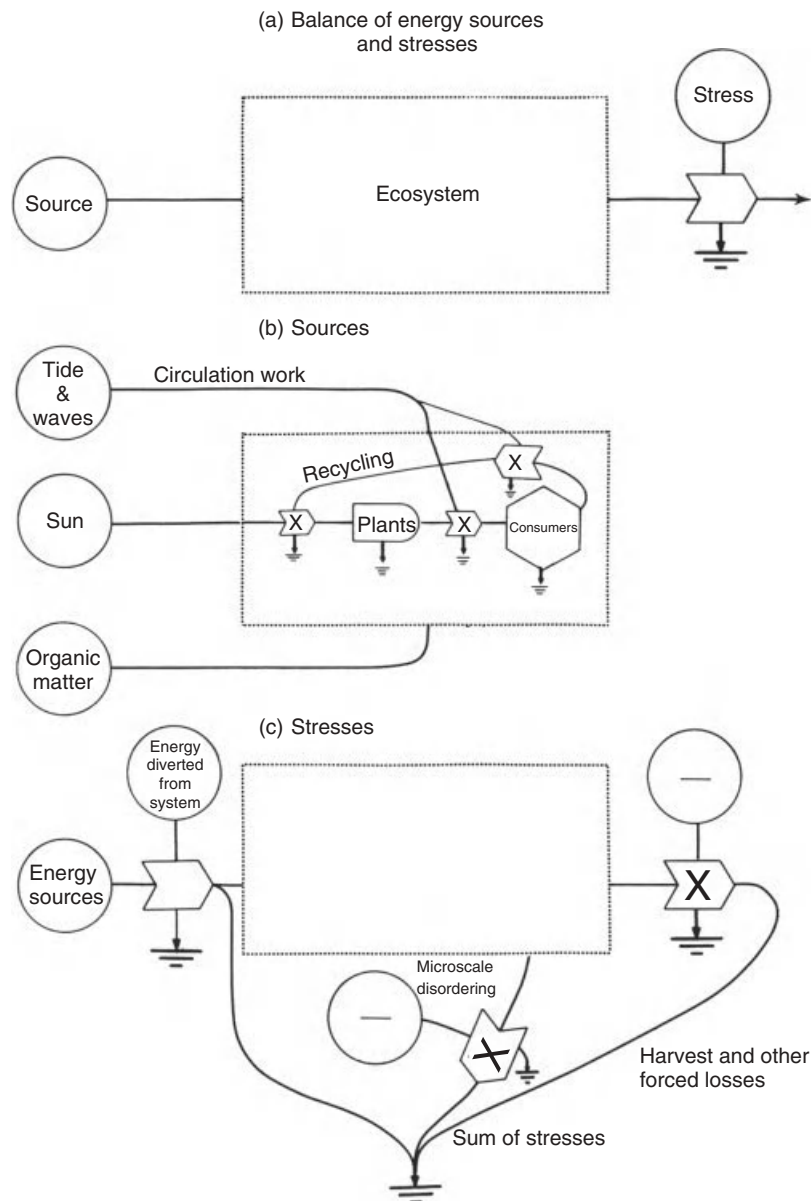
FIGURE 1.6 An energy-flow diagram illustrating how ordering and disordering energies are related in estuarine ecosystems. The status of an ecosystem results from a balance between energy sources, which build structure and order, and energy stresses, which cause a loss of structure and order (a). For estuaries, there are three main kinds of energy sources: sunlight, water movement (due to gravity, tides, and waves), and inputs of organic or inorganic nutrients (b). Three general kinds of energy stresses are (i) energy diverted from the system, (ii) microscale or entropic disordering, and (iii) harvest and other forced losses (c). See text for further discussion. *Source:* Figures from Odum and Copeland, 1972, used by permission.

eliminated and marsh productivity normally is lowered. A dam or river also can reduce the input of water and organic and inorganic matter entering an estuary. When the Aswan Dam was constructed in Egypt, the amount of river-borne material entering the estuary was drastically reduced, resulting in the collapse of the eastern Mediterranean sardine fishery that depended on the material.

The second kind of stress on estuarine ecosystems and their inhabitants is that due to microscale random disordering of the kind described by the second law of thermodynamics. This stress is the inevitable tendency of order and complexity to degrade into disorder and is characteristic of all living organisms. If an animal does not eat for a relatively short period of time, it dies because food is the potential energy

source it uses to maintain its internal order against this constant tendency toward disorder. The struggle against random disorder is a problem for all living creatures, and particularly for estuarine organisms, because much of the ordering energy available for estuarine organisms must be used to compensate for the large environmental variability. Human activity can aggravate the problem for estuarine organisms, for example, by the introduction of toxins, which tend to increase physiological "disorder" and thus make it even more difficult for an organism to cope with natural variability.

The last type of stress is forced loss. This means that potential energy within the system is removed before it can be used to do work. For example, the constant seaward flow of rivers and the action of tides flush material out of estuaries. Thus, water movement can be a stress as well as an energy source, and, most often, it is both. Human activities such as fishing and wetland destruction are also ways in which potential energy can be lost from an ecosystem.

Many estuarine organisms have evolved various behavioral and physiological adaptations to cope with stresses that would kill most other aquatic organisms (Vernberg and Vernberg, 1972, 1976). In doing so they are better able to exploit the available energy sources. These adaptations also allow organisms to use energies that would be stressful to most other organisms. For example, the small animals that live among the sand grains on a beach would be destroyed by the full force of the waves if they were not adapted to them, and meanwhile they use the oxygen and food that the waves pump through the sand. The *Rangia* clam of the oligohaline zone is adapted to high

siltation rates, periodic low oxygen, and extremely variable salinity and thus is able to live where it can use the large input of organic matter from the river without much predation or competition from other filter feeders. Many other examples of this type of adaptation are discussed throughout the book.

Because different estuarine systems and subsystems have characteristic energy stresses and sources, the biota of these various areas have adapted to these energies in different ways. These different energies and adaptations serve as the basis for the functional classification system of Odum and Copeland (Fig. 1.7). For most estuarine ecosystems, stress energies are moderate and similar so that the latitudinal variations in temperature and sunlight regime are the most important factors determining the distinguishing characteristics of these systems. Tropical, temperate, and polar estuarine ecosystems are conveniently distinguished. Solar energy input is highest and most regular in the tropics, but because of higher temperatures, there is more thermal disordering to overcome, so that tropical organisms have higher energy requirements. Seasonal changes are more distinct in temperate latitudes and the productivity of estuaries is concentrated into shorter periods of time; hence, seasonal "programming" of activities and migratory species becomes more important. At polar latitudes, ice and extreme cold are important stress energies.

When stress energies become large, either naturally or because of human activity, the associated biotic adaptations are, in a sense, similar over a wide latitudinal range. Thus, in these circumstances, the estuarine ecosystem can be classified according to the
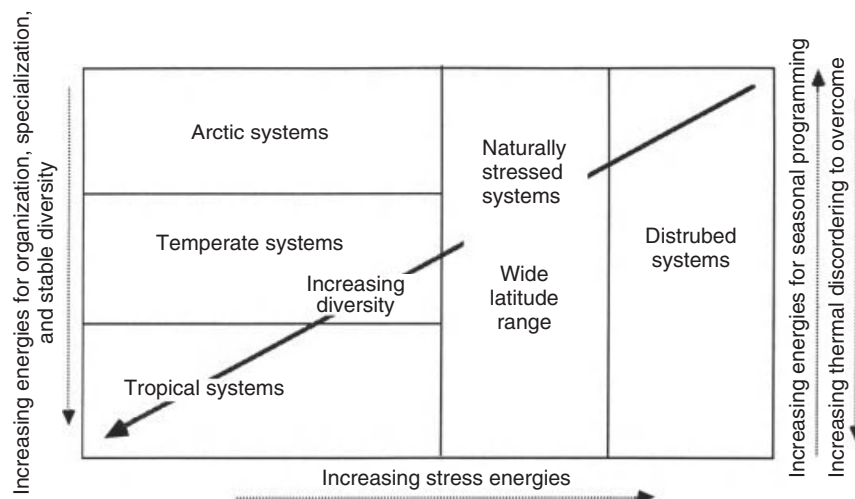
FIGURE 1.7 A functional classification of coastal ecosystems based on important energy sources and stresses. *Source:* From Odum and Copeland, used by permission.

characteristic stress. Sedimentary deltas, hypersaline lagoons, and beaches are natural examples of these types. Disturbed systems also develop due to human induced stresses and include eutrophied planktonic systems, organisms affected by toxins, and systems stressed by hydrologic changes (such as impounded marshes).

The energy input to coastal ecosystems is not constant but occurs in pulses. Pulsing is considered essential for most ecosystem functioning and has been called *nature's pulsing paradigm* (Odum et al., 1995). For example, understanding river ecosystems can be described in terms of the flood pulse (Junk and Bayley, 2008; Schram and Eggleton, 2006) and dynamic habitat interactions (Stanford et al., 2005). The functioning of coastal systems is affected by energetic forcings that serve to enhance productivity, increase material fluxes, and affect the morphology and evolution of these systems. This type of pulsing applies to many natural systems, but it is especially important for coastal ecosystems (Blum, 1995).

Eugene Odum (1980) recognized the importance of pulsing when he described estuaries as "tidally subsidized, fluctuating water-level ecosystems." But the tide is not the only energy subsidy to coastal systems. Energetic forcings occur over a hierarchy of different spatial and temporal scales (Day et al., 1995, 1997, 2000). These energetic events range from waves and daily tides to switching of river channels in deltas that occur on the order of every 1000 years and include frontal passages and other frequent storms, normal river floods, strong storms, and great river floods (Table 1.2). The primary importance of infrequent events such as channel switching, great river floods, and very strong storms such as hurricanes is in sediment delivery and in major spatial changes in geomorphology such as changes in river channels in deltas. More frequent events such as annual river floods, seasonal storms, and tidal exchange are also important in maintaining salinity gradients, delivering nutrients, and regulating biological processes. Throughout this book, the importance of these forcings is discussed for a variety of biotic communities and organisms and important processes.

1.5 ESTUARIES AND ESTUARINE ECOSYSTEMS IN A GEOLOGICAL CONTEXT

It is interesting to note that all of the estuaries discussed in this book did not exist 10,000–15,000 years

TABLE 1.2 A hierarchy of forcing or pulsing events affecting the formation and sustainability of deltas

Event	Timescale	Impact
Major changes in river channels	500–1000 yr	New delta lobe formation, Major deposition
Major river floods	50–100 yr	Channel switching Major deposition
Major storms	5–20 yr	Major deposition
Average river floods	Annually	Enhanced production Enhanced deposition Freshening (lower salinity) Nutrient Input Enhanced 1° and 2° production
Normal storm events (frontal passage)	Weekly	Enhanced deposition Organism transport Net transport
Tides	Daily	Drainage/marsh production Low net transport

Source: From Day et al., 1997, 2000.

ago and that they will cease to exist in the near geological future. The world's present estuaries were formed when sea level rose after the last glaciation. Since that time, they have been progressively infilled and will continue to be. Thus, present estuaries will, for the most part, cease to exist because they will fill up with sediment or because sea level will change again. However, estuaries will continue to exist at the edge of the sea, wherever it exists. At times like the present, when sea level is high enough to flood the edge of the continents, estuaries are widespread. When sea level was low enough so that the edge of the sea was on the continental slopes, as during the height of the glaciers, total estuarine area was small. The situation we see along the western coast of the Americas is the rule when sea level is low.

Of course the species and the types of biological communities that presently exist in estuaries have certainly existed for much longer than the estuaries themselves. Rivers have always flowed to the sea, whether it was higher or lower than at present. Estuarine ecosystems, with their characteristic species composition and adaptations, have moved back and forth with the edge of the sea. Therefore, even though particular estuaries are relatively short lived, estuarine organisms and estuarine ecosystems are very old.

1.6 HIGH PRODUCTIVITY: AN ESTUARINE FOCAL POINT

One of the things that makes the study of estuarine ecology so exciting is the lively discussion about what makes estuaries so highly productive. In this section, we outline some of these ideas, so that we have them in mind as we address the information in each chapter. The following discussion summarizes some current thinking about estuarine production. Perhaps we will view the idea very differently in 20 years.

1.6.1 Reasons for High Estuarine Primary Productivity: The Classic View

One of the most widely held beliefs by both estuarine scientists and others familiar with estuaries is that they are very productive per unit area. Sometimes, this means that the plants that exist in estuaries are very productive. At other times, it means that more organic matter is produced in estuaries than is used there or that estuaries are very productive of fish. Either way, this productivity is one of the key reasons why estuaries have attracted and sustained human populations throughout history.

What are the reasons for the supposed high productivity of estuaries? C.L. Schelske and E.P. Odum (1962) in a well-known paper entitled ''Mechanisms maintaining high productivity of Georgia estuaries'' stated that the estuaries of Georgia were among the most productive natural ecosystems in the world. They listed several reasons for this high productivity: (i) three types of primary production units (marsh grass, benthic algae, and phytoplankton), which ensure maximum use of light at all seasons; (ii) ebb and flow of water movements resulting from tidal action; (iii) abundant supplies of nutrients; and (iv) rapid regeneration and conservation of nutrients due to the activity of microorganisms and filter feeders. A number of these ideas have been discussed earlier in this chapter.

Now let us examine these points in more detail and consider the evidence on which they are based. There are, indeed, several distinct groups of primary producers in estuaries, many of which have high rates of primary production. A more general statement is that there is a diversity of sources of organic matter. In Georgia, there are three important producer groups: salt marsh grass, phytoplankton, and benthic algae. In other estuaries, sea grasses, mangrove swamps, and macroalgae may be important. Epiphytic algae grow on most surfaces in the euphotic zone. There is also input of organic matter from rivers and upland runoff.

High primary production measurements in Georgia and elsewhere led Schelske and Odum to conclude that ''estuaries are among the most productive natural ecosystems in the world.'' In Chapters 4–8 on estuarine primary production, we consider the factors controlling productivity and try to determine whether all estuaries actually do have extremely high rates of productivity relative to other ecosystems. Another reason for high productivity in Georgia estuaries, according to Schelske and Odum, is that there is significant year-round production. This has been observed in a number of estuaries at lower latitudes, but it is not true in higher latitude estuaries, which are often very productive but only during specific seasons.

Organic detritus from a variety of plant sources is abundant in many, if not most, estuaries, and many scientists argue that this detritus is an important food source. Most estuaries have an extensive autotrophic community, and there is often a surplus of organic matter available to consumers all year as organic detritus. The dynamics of organic detritus in estuaries has been the subject of a tremendous amount of research and controversy over the past several decades. In Chapters 9 and 10 on microbial ecology, in Chapter 16 on trophic dynamics of estuaries, and in the various chapters on estuarine consumers (Chapters 11–14), we consider estuarine trophic dynamics in detail.

Tidal action is considered to be an important factor contributing to high productivity. E.P. Odum once defined estuaries as ''tidally subsidized fluctuating water level ecosystems.'' Others have expanded on this to include other physical energies, including wind, waves, and riverine currents as well as tides. These factors produce very complex water movements in estuaries. In much of this book, we consider the nature of these physical factors, how they affect ecological processes, and how important they really are in ecological dynamics.

There are abundant supplies of nutrients in Georgia estuaries. Nutrient concentrations in estuaries are almost always higher than in the ocean and often higher than in freshwater systems. Schelske and Odum believed that most of these nutrients came from within the estuary and that they were responsible for the high levels of production. Some workers have emphasized the importance of rivers as sources of nutrients while others have not. Later, we discuss these two questions.

The final factor considered important was the rapid regeneration and conservation of nutrients.

Since most estuaries are relatively shallow and well mixed, there is a persistent intermingling of water and the bottom. This means that food in the water is available to organisms on the bottom and that nutrients released by benthic organisms are mixed throughout the water column. Some have argued that the combination of benthic regeneration and a shallow, well-mixed water column are the most important factors producing high estuarine productivity. The relative importance of different sources of nutrients is a topic of much discussion by estuarine ecologists and is presented in detail in Chapter 3.

As we indicated in the previous paragraphs, the factors listed by Schelske and Odum are still being discussed 40 years after their proposal. These issues have been the inspiration and focus of much research since then and are still a source of inspiration and controversy today.

1.6.2 Other Important Hypotheses about Estuarine Ecology

A number of other important hypotheses about estuarine function have been proposed and questioned and they help unify the study of estuaries. They are interrelated, but we separate them for the sake of clarity.

1. Intertidal wetlands are important to estuarine productivity because they (i) produce large quantities of organic detritus that is an important source of energy in estuaries and (ii) serve as an important nursery to the young of many marine and estuarine species. Many important chemical reactions take place in wetlands and thus estuarine chemistry is regulated by wetlands. Salt marshes and mangroves are covered in Chapters 6 and 7.

2. Organic detritus is exported from wetlands and serves as a very important food source for a wide variety of estuarine consumers. Recent evidence suggests that we may have to reexamine the importance of organic detritus. The importance of organic detritus is covered in a number of chapters in this book, especially Chapters 9 and 16.

3. Estuaries, especially those with extensive wetlands, support rich fisheries. There is considerable evidence showing both functional and empirical relationships between wetlands and fisheries. For example, the abundance of wetlands in estuarine regions is strongly correlated with regional fish catch. Very few fish are absolutely estuarine dependent, however, and so we have argued that the evidence is weak for estuary–fishery coupling, particularly wetland–fishery coupling. This issue is considered in Chapters 13 and 18.

1.7 HUMAN IMPACTS AND MANAGEMENT OF ESTUARINE ECOSYSTEMS

Humans have lived in and around estuaries for tens of thousands of years. Early peoples harvested the rich primary and secondary productivity of estuaries. Evidence of their presence includes village sites and middens or large accumulations of shells of harvested mollusks. As these piles of shells grew, they were often inhabited either seasonally or year round. About 5000 years ago, the first human civilizations developed adjacent to estuaries and lower river valleys. It is thought that the rich resources of the coastal margin provided an important energy subsidy that allowed the change from village-based agricultural societies to the complex social organization of civilization.

Throughout the Holocene, humans congregated near the coast and many of the world's current large cities such as New York, London, Amsterdam, Venice, Alexandria, Calcutta, and Shanghai developed near estuaries and deltas. These areas were an important source of food, and rivers provided important routes for navigation. Lower river valleys supported rich agricultural areas.

Humans have modified estuarine areas since the beginning of civilization. Notable preindustrial impacts include the draining of much of the Rhine delta by the Dutch and the elimination of most river input to Venice lagoon. But massive changes in estuaries mostly occurred in the twentieth century when human populations grew dramatically in the coastal zone. Human activity has physically changed coastal systems by draining and filling areas and by dredging channels for navigation, drainage, and access to minerals such as oil. Industrial, agricultural, and urban growth have introduced many toxic materials such as heavy metals and pesticides that poisoned estuarine organisms and nutrients and organic matter that led to eutrophication. Overharvest of commercially important organisms such as shrimps and introduction of new species, either accidentally or on purpose, has changed the composition of the biota.

As human impacts grew, so did the study of these impacts and efforts to reduce or mitigate them. Early efforts on estuarine management often dealt with solutions to specific problems such as reduction of the use of certain pesticides, advanced treatment of sewage, and restoration of wetlands. More recent management has focused on more comprehensive approaches such as ecosystem-based management and integrated coastal management. These topics are covered in more detail in Chapter 19.

1.8 THE POTENTIAL IMPACTS OF FUTURE TRENDS ON ESTUARINE ECOSYSTEMS

The twenty-first century will see the intensification of several major global trends that will strongly impact estuaries. Two important trends are global climate change and energy scarcity. Most now recognize that global climate change will dramatically impact society in the twenty-first century. Estuaries will be strongly impacted by climate change because most of the major climate impacts will directly or indirectly affect these ecosystems. Sea-level rise will impact coastal wetlands and humans living near the coast. For example, many, if not most, wetlands in estuaries may disappear as sea level rises, especially in deltas (Blum and Roberts, 2009; Syvitski et al., 2009; Vorosmarty et al., 2009). Changes in precipitation will affect the quantity and seasonality of freshwater inflow to estuaries affecting such processes as circulation, plant growth, and fisheries. Tropical storms (hurricanes and typhoons) will likely become more intense and will frequently lead to changes in estuaries and human activity adjacent to them. Rising temperatures will affect the distribution of many species. For example, during this century, the Gulf of Mexico will become completely tropical as mangroves replace salt marshes. Ocean acidification will affect the ability of some mollusks and corals to grow and survive. A detailed description of forecasted impacts of climate change are presented in Chapter 20.

A second major trend that will impact estuaries and how humans use them is energy scarcity. The availability of cheap fossil energy fueled the industrial revolution and spectacular growth of the human population and economy in the twentieth century. Humans acted as if fossil fuels were unlimited, but they are nonrenewable resources. It took millions of years to form the oil that will be used up in less than two centuries. There is strong evidence that about half of recoverable oil resources have been used and that conventional world oil production has peaked—this general topic is called *peak oil*. The implication is that oil will become progressively more expensive in coming decades. Since everything we do in society and as estuarine scientists is strongly tied to the use of oil and other fossil fuels, there are important implications for estuarine ecology because estuarine science and management are most often energy intensive. This is covered in more detail in Chapter 19.

1.9 HOW WE WILL PROCEED THROUGH THE BOOK

This book is designed to systematically carry the reader through the science of estuarine ecology. Chapters 2 and 3 introduce estuarine physical oceanography, geomorphology, and chemistry. Knowledge of these subjects is essential for a thorough understanding of the ecology of estuaries, because so much of the biology is related to such factors as water movement, sediment distribution, and chemical gradients. These two chapters are designed to both introduce the subjects and to put the information in the context of ecological processes.

The next sections of the book cover various aspects of the ecology of organisms that live in estuaries. In Chapters 4–8, we cover, respectively, phytoplankton, seagrasses, marshes, mangroves, and macroalgae of estuaries. In each chapter, the composition and distribution of the plants is discussed, and spatial and seasonal patterns of productivity and factors regulating productivity are analyzed. Chapters 9 and 10 are about estuarine microbial ecology covering metabolic controls of biogeochemical cycles and microbial food webs.

The sources, transport, and use of organic matter are topics that have generated considerable research and discussion over the past two to three decades and we try to capture some of this excitement. We cover zooplankton, benthos, nekton, and wildlife in Chapters 11–14, respectively. We discuss topics such as composition and distribution of biological communities, rates of secondary production, food habits, and factors regulating these communities. The following section of the book deals with ecosystem metabolism (Chapter 15), trophic dynamics (Chapter 16), and materials budgets (Chapter 17) of estuaries.

The final chapters include a discussion of the way humans have interacted with coastal systems. We cover interactions of people with estuaries focusing on fisheries and human impacts in Chapters 18 and 19. The impact of climate change on coastal systems is covered in Chapter 20 and the use of modeling to aid in understanding these systems is covered in Chapter 21.

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CHAPTER TWO

ESTUARINE GEOMORPHOLOGY AND COASTAL HYDROLOGY

Gregg A. Snedden, Jaye E. Cable, and Björn Kjerfve

2.1 INTRODUCTION

To understand the processes affecting the distribution and cycles of particulates, pollutants, nutrients, and organisms in estuaries, it is insufficient to focus solely on the biological and chemical aspects of the processes. Equally important are the water sources and movements (e.g., evaporation, precipitation, riverine discharge, submarine ground water discharge, wetland hydrology, and tidal exchange) as well as other hydrodynamic aspects of coastal systems, including circulation patterns, stratification, mixing and flushing; a careful consideration of the timescales of these processes needs to be included. When hydrodynamic changes occur quickly relative to biological, geological, and chemical transformations, they become the dominant controlling factors of many ecological processes in estuaries (Officer, 1980), and it is now widely recognized that a thorough understanding of marine estuarine ecology requires comprehensive knowledge and integration of physical processes affecting the system. This chapter is aimed at organizing, classifying, and describing some of these important physical characteristics and processes. The terminology will be that of a shallow-water oceanographer and, hopefully, this chapter will encourage future estuarine ecologists to use physical terms more precisely and consistently than has sometimes been the case in the past.

2.2 GLACIATION CYCLES

Present-day estuaries are geologically ephemeral coastal features. They formed during the last interglacial stage as sea level rose 120 m from 15,000 years ago to the present level, which was reached approximately 5000 years ago (Milliman and Emery, 1968; Fig. 2.1). Such glaciation and deglaciation events have occurred regularly during the past few million years, causing shifts in the position of the coastlines worldwide. The locations of estuaries have shifted accordingly.

Presently, estuaries are common coastal features, constituting as much as 80–90% of the coasts along the east and Gulf coasts of North America, but as little as 10–20% along the US Pacific Coast (Emery, 1967). Typically, estuaries are more abundant on coasts with broad flat continental margins than on coasts with narrow, steep continental margins (Schubel and Hirschberg, 1978).

During glaciation periods, a considerable fraction of the world's oceans were frozen into continental glaciers, and sea level was much lower than what it is
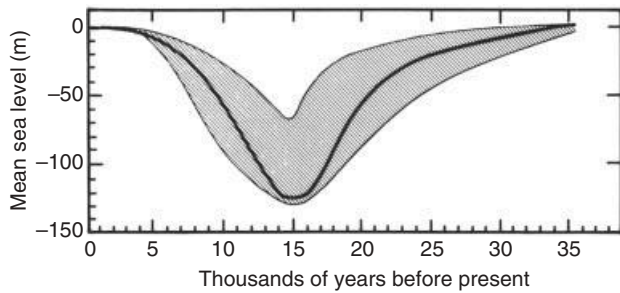
FIGURE 2.1 The variation of mean sea level for the past 35,000 years based on data from the Atlantic continental shelf of the United States: the solid line is the mean sea level and the dashed line is the envelope of all values. *Source*: Modified after Milliman and Emery, 1968.

FIGURE 2.2 Schematic representation of the continuum of inlet types from lagoons to deltas. *Source*: Modified from Davies, 1973.

now. Coastlines were then located on what is now the continental slope, and estuaries were both smaller and rarer. During interglacial periods, the glaciers melted, sea level rose worldwide, and estuaries became large and abundant (Schubel and Hirschberg, 1978).

The present situation of high sea level and extensive estuaries has existed for only 10–20% of the time during the past million years, for once formed, estuaries quickly fill with sediments and essentially disappear. The sediment sources are river-borne terrestrial materials from the eroding continents and net up-estuary movement of sand-sized materials from the continental shelf (Meade, 1969). From a geological viewpoint, the timescale of this infill is extremely short. Emery and Uchupi (1972) estimated that if sea level remained constant and all sediments were deposited into today's US estuaries, these would be filled within 9500 years, even if the load of the Mississippi River, which is half the nation's total, was not counted. But all estuaries obviously do not infill at this rapid rate, so that estuaries of various stages of geological development exist around the shorelines of the world (Schubel and Hirschberg, 1978). One major reason is that the sea level has been rising for the past 10,000 years. Another is that coastal erosional forces remove sediments from estuaries.

2.3 FROM LAGOONS TO DELTAS

The type and rate of geologic development of estuaries depend not only on glaciation cycles and local variations in sediment supply but also on a combination of other factors, including climatic variability, regional and local geology, and variability in marine energy inputs, particularly waves and tides impinging on the coast.

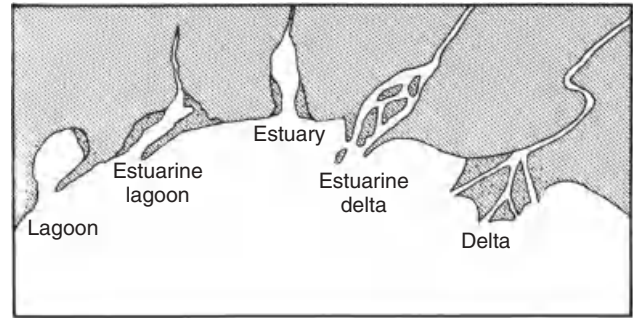According to the scheme of Davies (1973), there is a continuum of estuarine types (Fig. 2.2). At one end of the spectrum exist lagoons produced by marine (wave) action, found typically behind a barrier, and characterized by sand-sized sediments. Good examples of this type of environment are the lagoons of the southern Texas and Mexican Gulf coasts (Lankford, 1976). At the opposite end of the spectrum lie deltas. They are produced by river processes rather than by marine activities. They typically protrude into a receiving basin and are characterized by fine-grained silty sediments from terrestrial runoff. Between lagoons and deltas lie estuarine lagoons, estuaries, and estuarine deltas, representing a mixture and gradation of the two extreme coastal environments. Presumably, a decrease in wave energy coupled with an increase in river sediments would shift a particular system from the lagoon extreme toward a delta extreme. Estuaries have probably shifted in such a manner throughout geologic time as climates have changed.

2.4 DEFINITION

2.4.1 A New Definition

The existing definitions of estuaries are neither satisfying nor useful to the modern problems of estuarine ecologists or to the diversity of environments considered above. Thus, a new functional definition is proposed, which will hopefully help those who work with the spectrum of estuarine types, including lagoons, river mouths, and deltas. An estuarine system is a coastal indentation that has a restricted connection to the ocean and remains open at least intermittently. The estuarine system can be subdivided into three regions:

1. A *tidal river zone* or fluvial zone characterized by lack of ocean salinity but subject to tidal rise and fall of sea level.
2. A *mixing zone* (the estuary proper) characterized by water mass mixing and the existence of strong gradients of physical, chemical, and biotic quantities reaching from the tidal river zone to the seaward location of a river mouth bar or ebb-tidal delta.
3. A *nearshore turbid zone* in the open ocean between the mixing zone and the seaward edge of the tidal plume at full ebb tide.

This definition differs considerably from those previously proposed in that it recognizes and includes a nearshore marine component, estuarine in character, which should be considered in the treatment of the physical or chemical dynamics, or ecology, of the estuarine system as a whole. Thus, our definition of estuaries includes the adjacent coastal waters.

Dionne (1963) and Fairbridge (1980) chose to subdivide the mixing zone into an upper and lower region somewhat arbitrarily, and Hansen and Rattray (1965) subdivided the same zone into three dynamic regions. Such subdivisions can, of course, be made when the need arises, depending on the particular applications or local conditions.

2.4.2 Dynamic Boundaries

It should be recognized that the boundaries of the three zones listed above are dynamic. They change positions continuously, on timescales from shorter than a tidal cycle to annual cycles to geologic timescales. The landward extent of the tidal river zone moves downriver with increasing freshwater discharge, and as the tidal amplitude changes from spring to neap tide. Similarly, the interface between the tidal river and mixing zones oscillates over the tidal cycle and moves seaward with increasing river runoff. The interface between the mixing and nearshore zones changes much more slowly since it is the edge of the land, usually only on timescales longer than the seasonal cycle and most dramatically over thousands of years. A severe storm, however, could breach a barrier island or reef (Hayes, 1978) and thus dramatically relocate this interface overnight. The seaward boundary of the nearshore zone will change positions depending on the stage of the tide, river discharge, and prevailing oceanographic and meteorological conditions.

In a given system, all zones may not be present. For example, lagoons in arid or semiarid coastal regions with a small tidal range may not exhibit a tidal river zone. An example of such a system is Cancun Bay, Mexico, on the Caribbean side of the Yucatan Peninsula. A given estuarine/lagoon system may not exhibit a mixing zone, as defined, if the river discharge is very large. In that case, the tidal river could border directly on the nearshore zone so that freshwater leaves the river mouth with no mixing with salt water and the estuarine mixing processes would actually take place within the nearshore zone. Examples of such systems are the Amazon River (Gibbs, 1970) and many large rivers at flood stage. Finally, the nearshore zone may be nonexistent in lagoons such as Cancun Bay, where the tidal range is small and there is a lack of freshwater and sediment discharge. A particular estuary can, in theory, go through cycles so that the system alternately consists of one, two, or three of the defined zones on a seasonal basis.

2.4.3 Some Exceptions

Because an estuary is defined as "a coastal indentation," semienclosed inland seas such as the Baltic and the Mediterranean systems in their entirety are not included in the definition, nor are estuary-like systems that connect to large lakes rather than to an ocean (e.g., the Sea of Azov, which adjoins the Black Sea).

The large hypersaline (300 ppt) lagoons on the eastern shore of the Caspian Sea may be expected to exhibit processes similar to those operating in coastal lagoons (Klenova, 1968). Because these inland lagoons are emptied of water by severe wind action for half the year, the dynamics and ecology of the Caspian Sea systems are very different from the typical coastal lagoon. Some western Australia coastal salt flats/lagoons that flood probably behave similarly.

2.4.4 Water Balance

Pritchard (1952a) proposed a classification of estuaries based on their water balance. He gives three classes: (i) positive estuaries, where the combined freshwater input from rivers, ground water, and rainfall exceeds evaporation; (ii) neutral estuaries, with a balance between evaporation and freshwater input; and (iii) negative or inverse estuaries, where the evaporation exceeds the combined freshwater input.

Most readers would think that "estuary" means what Pritchard calls a positive estuary and that a coastal lagoon means a negative estuary. Depending on the hydrologic cycle, a system could change seasonally from being positive to negative or vice versa. The neutral estuary is not an important stage but represents a temporal transition of a system between positive and negative stages.

Although it may at times be useful to think of coastal systems in terms of the water balance, this means of classifying an estuary is no longer in common use. With the exception of lagoons in arid or semiarid regions, most estuaries are positive. In fact, the traditional definition of an estuary (Cameron and Pritchard, 1963; Pritchard, 1967) as ''a semienclosed coastal body of water with a free connection with the open sea within which sea water is measurably diluted by freshwater from land drainage'' defines an estuary as a positive estuary. It certainly represents the estuarine system most commonly studied. It is, however, a much too restrictive definition in that it excludes negative estuaries, the tidal river, or nearshore zones. Using this definition, a system does not remain an estuary during high runoff conditions when the mixing zone disappears, as in the case of the Mississippi River floods or the Amazon River at all times.

2.5 GEOMORPHIC CLASSIFICATION

2.5.1 Estuarine Types

It is more useful to classify estuaries according to their geomorphology. Each geomorphic type exhibits at least a somewhat similar dynamic behavior in terms of water circulation and mixing. Surface water estuaries can be divided into five main groups (Pritchard, 1952b; Dyer, 1973): (i) coastal plain estuaries, (ii) deltaic estuaries, (iii) lagoons (or bar-built estuaries), (iv) fjords, and (v) tectonically caused estuaries. Another estuarine system often overlooked but no less important to the biogeochemical cycling and ecology of coastal water bodies is the (vi) subterranean estuary first conceptualized by Moore (1999).

2.5.2 Coastal Plain Estuaries: Classical

Coastal plain estuaries have been studied most extensively because they are the most common type in regions where studies began. They formed during the last eustatic sea level rise, when river valleys became increasingly more flooded by the melting glaciers. Thus, they exhibit the geomorphic characteristics of river channels and flood plains and are sometimes called *drowned river valley estuaries*. The typical cross section of a classical coastal plain estuary consists of a V-shaped channel, seldom deeper than 20 m, bordered by broad shallow flats (Figs 2.3 and 2.4). Coastal plain estuaries vary greatly in size up to that of the Chesapeake Bay, some 25-km

long and on the average 25-km wide, the largest US coastal plain estuary. Other good examples of large coastal plain estuaries are Delaware Bay and Charleston Harbor, South Carolina. Others have been described by Officer (1976) and Dyer (1973).

2.5.3 Coastal Plain Salt Marsh Estuaries

Another kind of coastal plain estuary, salt marsh estuaries or salt marsh creeks, is found commonly along much of the US East Coast, particularly from Cape Fear, North Carolina, to Cape Canaveral, Florida. They are characterized by the lack of a major river source but have a well-defined tidal drainage network, dendritically intersecting the extensive coastal salt marshes. These estuary–marsh systems are usually interconnected. Water and material exchanges between the system and the coastal ocean occur through narrow, tidal inlets, which continuously change their configurations, sometimes dramatically, on timescales of less than 10 years (see Brunn, 1978). Although these systems formed in a manner similar to lagoons, they have infilled to a much greater extent, and now consist primarily of subaerial or intertidal salt marshes. The estuary proper in these systems consists of the drainage channels. These typically occupy less than 20% of the system area and resemble dynamically the classical coastal plain estuary. The size of the estuary is proportional to the size of the marsh drained. The typical cross section usually exhibits two deep channels separated by a shallow region. Channel depths seldom exceed 10 m although it is known that localized, deep scour holes in excess of 25 m commonly occur at the junction of tidal creeks (Kjerfve et al., 1979).

2.5.4 Deltaic Estuaries

In contrast to drowned river valley and salt marsh estuaries described above, deltaic systems provide home for expansive fresh, brackish, and salt marshes and mangroves. These systems are characterized typically by major river systems, such as the Ganges–Brahmaputra–Menga (India), the Mekong (southeast Asia), the Nile (Egypt), and the Mississippi (USA) rivers. As the main river approaches the coastline, the water velocities slow and water is moved out across the deltaic system. Distributary channels can facilitate this movement into the estuarine wetland environment, or the river may overbank and flow as overland flow across the landscape. These distributary channels radiate from the main river source in a dendritic network and provide a large and generally shallow (<5 m) estuary to support primary productivity and large nursery grounds for marine
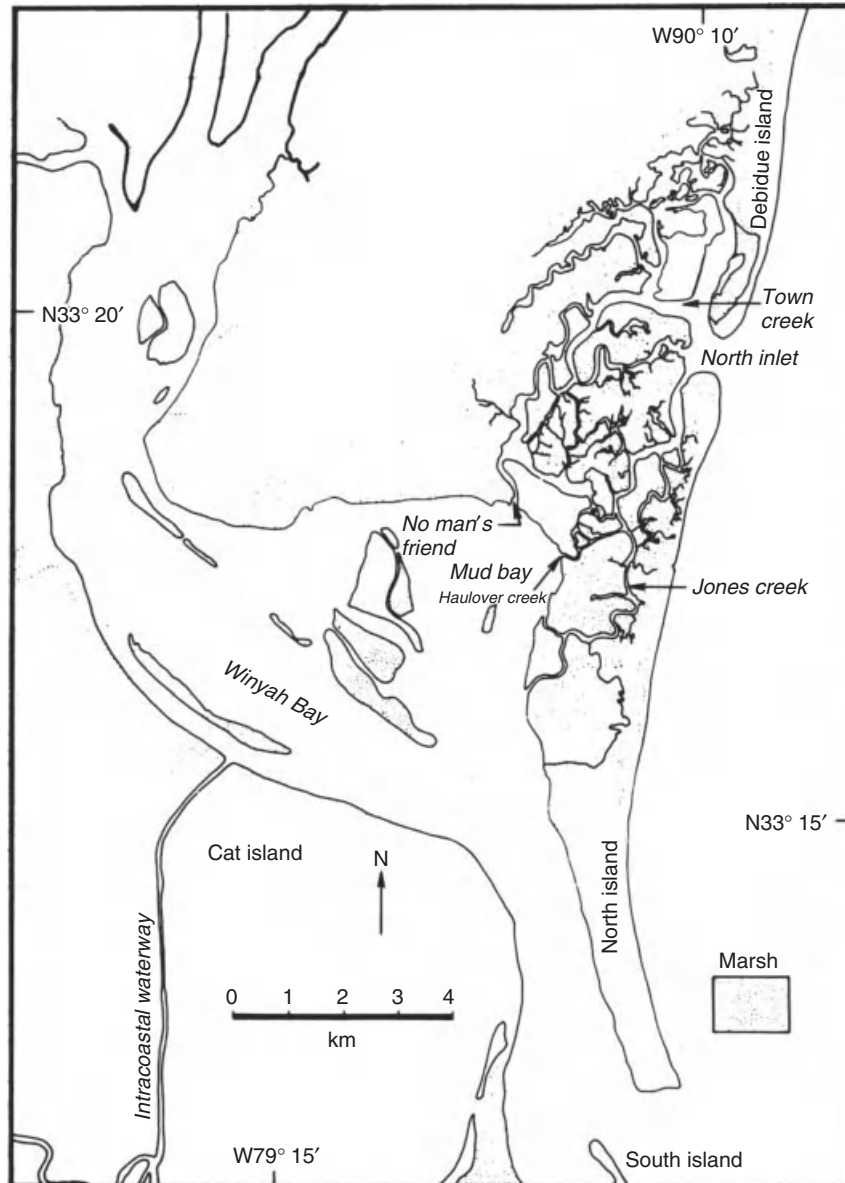
FIGURE 2.3 Examples of coastal plain estuaries: Winyah Bay and North Inlet, South Carolina. Winyah Bay is a classical coastal plain estuary, whereas the North Inlet system is a coastal plain salt marsh estuary.

and fresh fisheries. Spring discharge following winter snowmelt or tropical wet season precipitation may also cause overbank flooding and crevasses that seasonally refuel the systems with nourishment in the form of nutrients and sediments. Rivers generating these deltaic estuaries are typically greater than 15-m depth and discharge 1180 m^3/s (*Nile R.*) to 156,000 m^3/s (*Amazon R.*) annually (Vorosmarty et al., 1998). Deltaic estuarine areas can range in size from 81 km^2 in the salt marshes of the Santee River, South Carolina (Prevost, 2004) to 13,500 km^2 in the mangrove wetlands of the Ganges–Brahmaputra

Delta (Islam and Gnauck, 2008) and represent some of the most productive, yet fragile, estuaries worldwide. High population growth, coastal urbanization, and upstream hydrologic manipulation along river corridors have contributed to deltaic deterioration in the past 100 years (Syvitski et al., 2009).

2.5.5 Lagoons

Whether salt marsh estuaries are classified as "coastal plain estuaries" or "lagoons" is rather unimportant and certainly arbitrary. Lagoons exhibit a larger fractional area of open water compared with, for
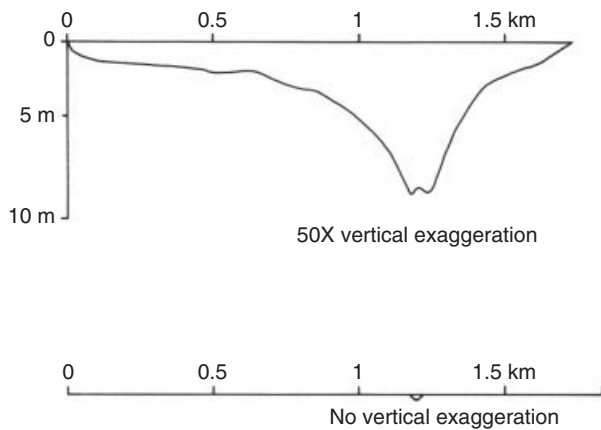
FIGURE 2.4 Cross-sectional profiles of an arbitrary coastal plain estuary, showing the same section in 50 times vertical exaggeration (top) and without any vertical exaggeration (bottom). Coastal plain estuaries have very wide and shallow cross sections. When these sections are presented with vertical exaggeration (which is most often the case), this gives a misleading impression.

example, southeastern salt marsh estuaries. Whereas lagoons are oriented parallel to the coast, coastal plain estuaries are most often orientated normal to the coast (Fairbridge, 1980; Fig. 2.5). Lagoons have a less well-drained subaqueous drainage network and are uniformly shallow, often less than 2-m deep over large expanses. The physical processes of lagoons are mostly wind dominated, whereas diffuse freshwater inflow and tide tend to dominate salt marsh systems, at least in the southeast region of the United States. Nevertheless, the origin of lagoons is similar to that of the southeastern salt marsh estuaries (Lankford, 1976).

During the interglacial stage, 80,000 years ago, the Pleistocene shoreline stabilized some 6 m above the present mean sea level, leading to the formation of a narrow raised ridge system parallel to the coast. The ridge is most commonly a sand barrier, as in the case of Laguna de Terminos, Mexico, or a coral reef barrier, as in the case of the Belize barrier reef lagoon on the Caribbean side of the Yucatan Peninsula. Then, during the lowered level of the last glacial period, atmospheric and fluvial processes eroded much of that earlier coast. As sea level again rose to its present level, extensive areas behind the remnants of the raised ridge flooded, while marine and atmospheric processes maintained and reshaped the barrier ridge (Lankford, 1976). Sedimentation processes then caused the systems to infill differentially, and estuary shapes were further modified by climate and vegetation.

In contrast to most estuaries, lagoons can exhibit a wide range in water residence times due to their parallel orientation to the coast and variability in their connections to ocean. Smith (1993) reported residence times for the Indian River Lagoon, on the east Florida coast (USA), which ranged from a few weeks close to inlets to as great as 6 months to a year in the most northern reaches of the lagoon. This lagoon is over 240-km long and ocean inlets are all positioned in the southern portion of the lagoon, thereby limiting exchange. In Terminos Lagoon, Yucatan Peninsula (Mexico), residence times are generally much shorter (4 weeks to 7 months) due to the coastal current, which sweeps in the north inlet and out the south inlet, and also to the wet and dry seasons (Yáñez-Arancibia and Day, 2006).

True lagoons are common on all continents and are far more prominent than the sparse literature implies. In North America, for example, they fringe eastern Florida and the Gulf of Mexico and are abundant on the Pacific coast of Mexico and southern coast of Brazil. The physical characteristics and dynamics of a few have been described by Smith (1987, 1993), Möller et al. (2001), Lankford (1976), Castanares and Phelger (1969), and Collier and Hedgpeth (1950). But, other studies of lagoons are rare; several have been studied in other countries: the Coorong in South Australia (Noye, 1973, Noye and Walsh, 1976), St. Lucia lagoon in South Africa (Orme, 1974, Orme and Loeher, 1974), and those of southeastern Australia (Bird, 1967).

2.5.6 Fjords: Classical

Fjords also owe their origin to the glaciation cycle. During the advance of continental glaciers, tongues of the leading ice edge scoured out many river valleys in latitudes above 45° (Fairbridge, 1980; Dyer, 1979). Where the ice edge reached its most seaward extent, on what was then a portion of the continents, a steep rock bar usually had formed seaward of the leading ice edge. It was there for two reasons. First, the ice had not yet been able to scour it away, in part because the ice began to float on the salt water. Second, scoured material from the basin was pushed forward by the advancing glacier and deposited at the leading ice edge. When the glaciers retreated, these rock bars remained to provide spectacular relief at the seaward edge of the basins themselves. Whereas the present water depth over sills generally varies from 10 to 90 m, the depth of the interior fjord basins often exceeds 800 m. The overdeepened portion of the basins commonly extends several hundred kilometers inland. A further geomorphic characteristic of fjords
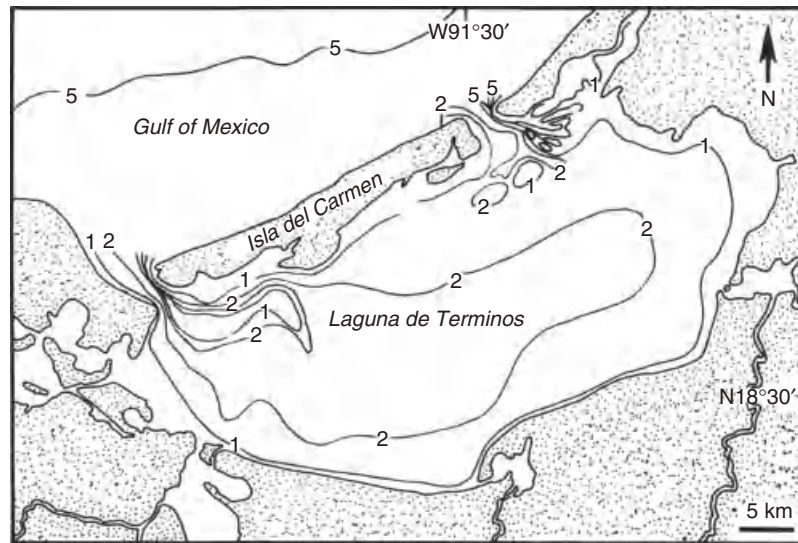
FIGURE 2.5 Example of a lagoon, Laguna de Terminos, Campeche, Mexico. Isobaths in meters are drawn and indicate that the lagoon for most parts is only 2-m deep. *Source*: Modified after Gierloff-Emden, 1977.

and glacially carved inlets is their V-shaped cross-sectional form, due to the glacier scour.

Fjords and glacial inlets are common in both hemispheres where there has been glacial activity. They are particularly spectacular on coasts that serve as leading edges of tectonic plate margins, called *subducted coasts*. Good examples are the fjord inlets of southern Chile (Pickard, 1971), Alaska, British Columbia (Pickard, 1956; Fig. 2.6), and New Zealand. Fjords also occur on the present or formerly glaciated coasts of Norway, Spitsbergen, Greenland, and Graham Land in Antarctica (Fairbridge, 1980). A useful treatment of the oceanographic features of Norwegian fjords is that of Saelen (1967).

2.5.7 The Fjord-Like Fjärd

Closely related to fjords are fjärds (Swedish) or firths (Scottish). These occur commonly in southern Sweden, eastern Canada and New England, and Scotland, where the continental relief is less spectacular and the continental shelf is more extensive compared with a subducted margin coast (Fairbridge, 1980). Fjärds or firths also formed as a result of glacier scour but do not exhibit the overdeepened basin or the V-shaped profile. Water depths are much shallower than for fjords, usually on the order of tens of meters. The shallow water depth, particularly in the case of Swedish fjärds, is due at least partially to the quick isostatic rebound of the continent, a response to the cessation of ice loading. This uplift rate has been measured as high as 15 m per 1000 years.

2.5.8 Tectonically Caused Estuaries

The fourth and final geomorphic classification category occurs on tectonically active coasts. These are the estuaries caused by faulting, graben formation, landslide, or volcanic eruption. The best and most extensively studied estuary in this group is San Francisco Bay (see Officer, 1976; Conomos, 1979). Tectonically caused estuaries exhibit much variability and different ones may behave oceanographically similarly to coastal plain estuaries, fjords, or lagoons, depending on the local constraints. In summary, estuaries are formed by specific physical processes. The extensive nature of estuaries today is due in large part to the extensive glaciation of 10,000 years ago.

2.5.9 Subterranean Estuaries

Analogous to salt wedge surface water estuaries, subterranean estuaries represent the interface between seaward discharging groundwater from coastal aquifers and landward moving sea (Fig. 2.7). Groundwater plume are less dense and rise as they encounter infiltrated seawater in coastal sediments. This subterranean estuarine system exists wherever aquifers hydraulically intersect coastal water bodies (Cooper, 1959; Johannes, 1980; Moore, 1999) and is characterized by longer residence times, greater water–particle interactions, lower dissolved oxygen concentrations, and strong biogeochemical gradients. Consequently, chemical reactions (e.g., diagenesis) and water circulation patterns within this porous and/or permeable media are more complex than in surface estuaries. Submarine groundwater discharge
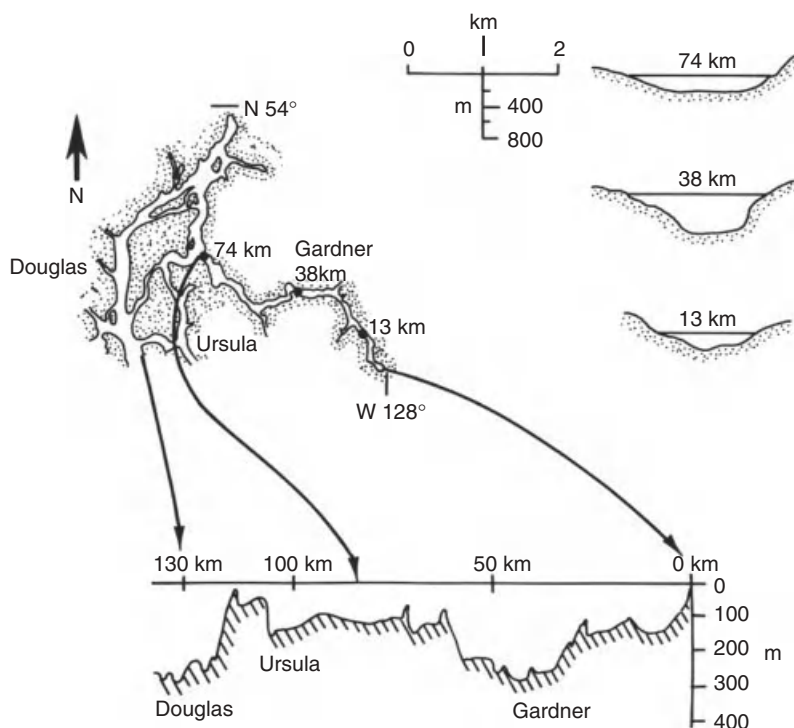
FIGURE 2.6   Example of a fjord, the Gardner system in British Columbia, Canada. *Source*: Modified after Pickard, 1956.

(SGD) may include both meteoric groundwater from continental aquifers and pore water exchange from marine physical and biological processes (Taniguchi et al., 2002; Burnett et al., 2003; Martin et al., 2006; Martin et al., 2007). The magnitude of meteoric sources to coastal waters varies greatly depending on local climate, geology, and consumptive groundwater use by coastal communities, whereas the magnitude of marine sources to SGD varies depending on local wind stress and tides, resident benthic burrowing organisms, bottom topography, and sediment type (Cable and Martin, 2008).

Subterranean estuaries can exist within surface water estuaries and, consequently, can contribute to their hydrologic and biogeochemical budgets. Subterranean estuaries have been identified and studied in Waquoit Bay, Massachusetts (Michael et al., 2005), Indian River Lagoon (Martin et al., 2007) and at Turkey Point (Santos et al., 2008) both in Florida, the South Atlantic Bight (Moore and Wilson, 2005; McCoy et al., 2007), North Inlet, South Carolina (Wilson and Gardner, 2006), Flamengo Bay, Brazil (Burnett et al., 2006; Cable and Martin, 2008; Povinec et al., 2008), Cockburn Sound, Perth, Australia (Burnett et al., 2006; Loveless, 2006), Mauritius (Oberdorfer, 2005; Burnett et al., 2006), and Osaka Bay, Japan (Taniguchi and Iwakawa, 2004) to name a few regions

in the United States and worldwide. These studies differ in the lateral extent of the subterranean estuary with most appearing within 10–20 m of the shoreline. However, convective circulation may also yield a quasi-subterranean estuary on the continental shelf in response to interactions between deep confined aquifers and the overlying shelf waters, as shown within 8 km of coast in the South Atlantic Bight (Moore and Wilson, 2005). In addition, the biogeochemical flux associated with this category of subterranean estuary may be more important than surface estuaries in some cases. Charette and colleagues (2005) and Charette and Sholkovitz (2006) demonstrated that the fresh–saline seepage front caused by subterranean estuaries is also responsible for an ''iron curtain'' of metal diagenesis, while other studies have shown the significance of this discharge for nutrient fluxes to coastal water bodies and the ocean (Krest et al., 2000; Santos et al., 2008). Groundwater inputs and their dissolved constituents are also considered responsible for local biological zonation in coastal water bodies by either preferentially excluding or encouraging flora and fauna growth (Kohout and Kolipinski 1967; Miller and Ullman 2004). Effects of subterranean estuaries, and their hydrologic and chemical consequences, are beginning to be recognized for coastlines all over the world.
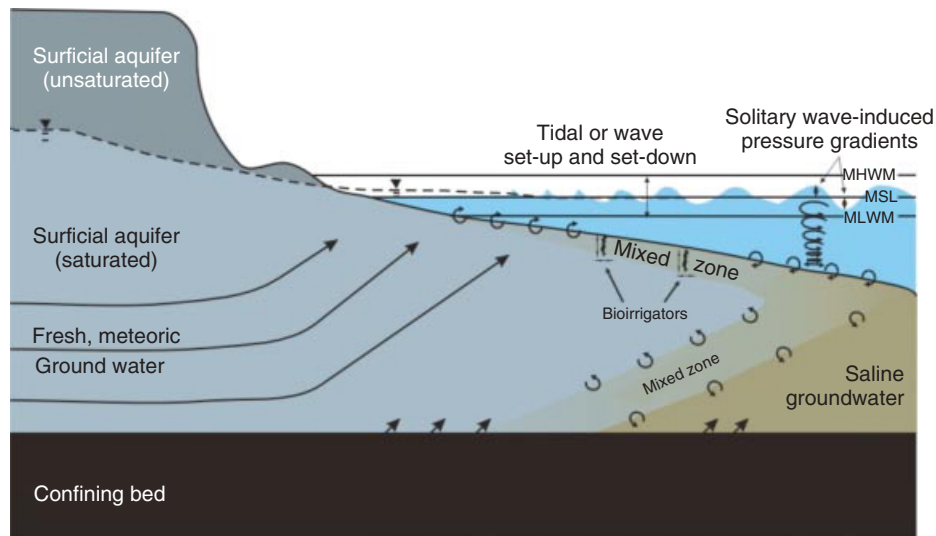
FIGURE 2.7   One example of a generalized subterranean estuary, where fresh meteoric groundwater mixes with infiltrated seawater. *Source*: Modified from Smith et al., 2008.

2.6 CIRCULATION

2.6.1 Estuarine Circulation

Estuarine water circulation is a physical process that affects or controls many ecological processes. For example, the residence time of a given parcel of water in an estuary is a function of the circulation patterns, and the ratio of water residence time to biogeochemical turnover rate indicates the degree to which hydrodynamics dominate or modify estuarine processes.

Thus, computation of fluxes of dissolved constituents such as nutrients, pollutants, and salt, as well as of particulate materials such as sediments, detrital matter, and plankton, requires knowledge of the circulation. It is common to simulate estuarine physical processes with rather complex mathematical equations. But reasonable formulations for such equations usually can be achieved only after making several simplifying assumptions, and these assumptions depend very much on the assumptions we make about circulation. Very often the complexity of the real systems makes it difficult for us to produce realistic results from our simplified models. Also, the estuarine bathymetry is a function of the circulation, and in turn, the circulation depends on the bathymetry (Kjerfve, 1978). Thus, care must be exercised in using estuarine hydrodynamic information. As shown subsequently, the fact that the circulation causes water to move in a certain direction does not necessarily mean that dissolved and particulate constituents will move in the same direction.

Estuarine circulation normally is defined as the residual water movement, meaning that short-term effects are averaged out. Because water motions occur on a continuum of timescales, it is critical to choose the appropriate time duration over which to estimate these residual currents. Thus, our computations of circulation depend greatly on the average timescale used. As most of the current variability usually occurs with a tidal periodicity, estuarine circulation is usually calculated as the residual water movement after the currents are averaged over one, two, or numerous complete tidal cycles. It is important to realize that the circulation can never be determined from a single set of instantaneous measurements but represents a calculated quantity that requires systematic measurements over an extended time period for its determination (Kjerfve, 1979).

The time-averaged currents that make up the circulation vary depending on location in the estuary and the particular depth at which an estimate is made. It is common practice to refer to these time-averaged currents as net currents, tidal currents, tidal residuals, or nontidal flows.

2.6.2 Types of Estuarine Circulation

The energy that drives estuarine circulation is derived from either solar heating or gravitational attraction between the moon and sun on the one hand and the ocean waters on the other.

Solar heating differentials also cause wind, rainfall, and ocean water temperature differences. Rainfall, in particular, affects estuaries by the energy and mass associated with freshwater inflow

from rivers, and these are major processes driving estuarine circulation. Estuarine circulation is also driven by wind stress on the estuarine water surface, a second major force driving estuarine processes.

Gravitational attraction on the sea by the moon and the sun is the third important process driving the estuarine circulation, which is responsible for the regular rise and fall of the tide and the more complex oscillatory water currents.

Although wind waves generated within an estuary or swells propagating into an estuary from the ocean could conceivably cause or alter circulation, such waves are normally not very important. But variability in nearshore current structure has a modifying effect on estuarine circulation, as is discussed later.

Two other factors are important in determining circulation—estuarine geometry and bathymetry (i.e., curvature and friction effects). Both effects are capable of modifying circulation significantly, but they differ from the driving forces discussed above in that they are passive, that is, these factors alter the flow pattern only when currents already exist. Similarly, ice cover on high-latitude estuaries and human activities (e.g., dredging, channelization, damming, and diversion) can alter induced circulation patterns.

The three main driving forces are each responsible for a particular circulation type respectively: (i) gravitational circulation (due to freshwater runoff), (ii) tidal circulation, and (iii) wind-driven circulation. Each type is discussed in more detail later. Although a given estuary usually is dominated by one circulation type, this may change temporarily. In addition, two or three different circulation types could, in fact, be in operation simultaneously in the same estuary.
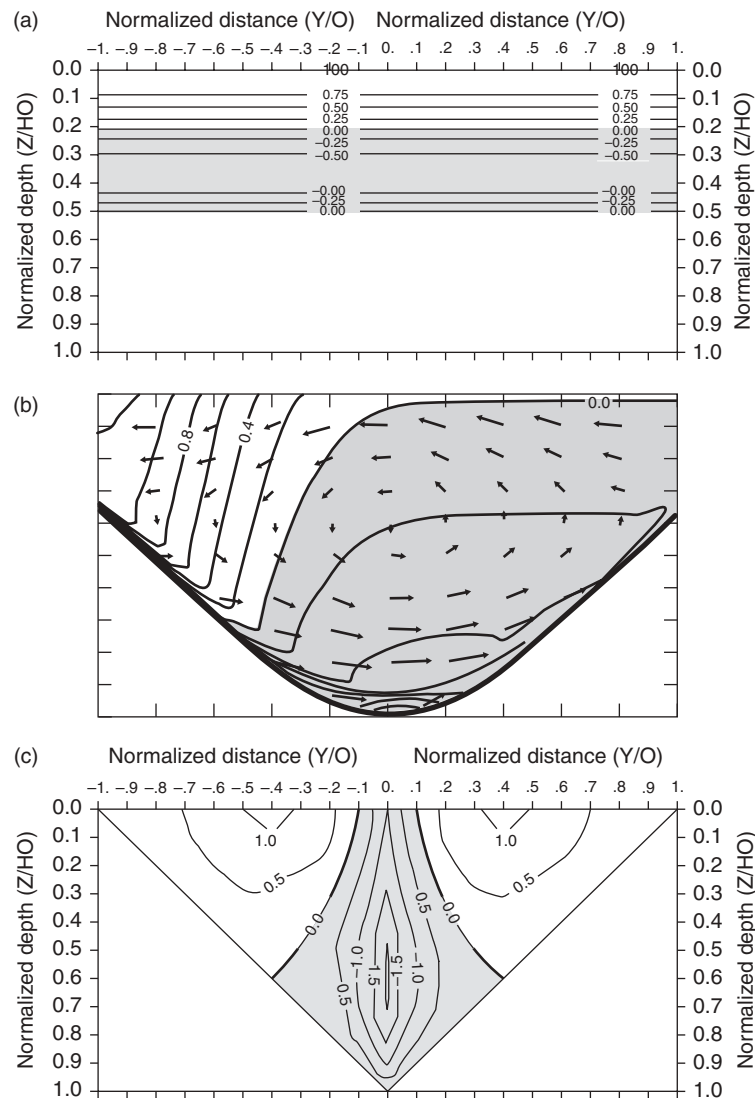
2.6.3 Gravitational Circulation

The presence of salt in an estuary produces a horizontal density gradient, where relatively freshwater near the head of an estuary is less dense than saltier water near the mouth. This density gradient results in increased ebb tide velocities near the surface and increased flood tide velocities near the bed. When averaged over a tidal cycle, the resulting residual currents transport saline waters landward in the deeper regions of the water column and fresher waters seaward near the surface. This two-layer flow pattern (Fig. 2.8a), called *gravitational circulation* due to the fact that it is driven by gravity acting on density differences within an estuary, was first described by Pritchard (1956), Pritchard and Kent (1956), and Dyer (1974) and was represented in an elegant mathematical solution by Rattray and Hansen (1962) and Hansen and Rattray (1965).

Velocity shear across the two layers can result in entrainment of saline waters from the lower layer into the seaward-flowing upper layer, resulting in discharges in the surface layer at the estuary mouth that are 10–20 times greater than freshwater inputs at the estuary head. Thus, much more water takes part in the gravitational circulation than was introduced as freshwater runoff. For example, if the river discharge into an estuary is $R\,\mathrm{m^3/s}$, and the longitudinal density gradient forces $24R$ $\mathrm{m^3/s}$ of saline water to flow landward into the estuary in the lower layer, the near-surface layer discharge at the estuary mouth must be $25R$ $\mathrm{m^3/s}$ for the volume of the estuary to remain constant.

Although gravitational circulation in estuaries is related primarily to the salinity distribution, the temperature distribution can drive the circulation just as well under certain conditions. In temperate and tropical estuaries, salinity alone usually determines the water density (Kjerfve, 1979), because the freshwater inflow provides a source of less dense water that mixes with dense ocean water only slowly. Usually, no equally effective temperature source or sink occurs, which could create as large a density difference. An exception to this generality may be found in certain arctic or subarctic estuaries where very cold and thus, relatively dense, freshwater flows into a less cold ocean. In this case, the temperature structure may be as important as the salinity in driving the gravitational circulation of an estuary. Pickard and Trites (1957) showed that a number of inlets in British Columbia, Canada, had this characteristic.

Although gravitational circulation generally occurs with light, relatively freshwater flowing seaward over a denser, saltier, landward-flowing layer, under certain circumstances, this pattern can be inverted. In shallow lagoons, high evaporation rates caused by wind stress and solar heating can result in a wide range of salinities (15 to as high as 90; Noye, 1973), even over short time periods (less than a week). Often, this evaporation causes elevated salinities that far exceed those over the adjacent shelf. The typical estuarine salinity gradient is thus reversed, and these circumstances can induce reversed gravitational circulation, where less saline shelf waters flow into the estuary on the surface and outflow of hypersaline lagoon waters to the shelf occurs near the bottom of the estuary cross section (Wolanski et al., 1981). This phenomenon has also been observed in estuaries that lie down-coast from large river mouths. During high discharge, the plume of the nearby river can be confined to the nearshore areas under downwelling-favorable wind conditions, causing salinities inside nearby estuaries to exceed

FIGURE 2.8 (a) Idealized gravitational circulation in an estuary with rectangular cross section (modified from Wong, 1994). (b) Idealized gravitational circulation taking into account effects of rotation and interactions between bathymetry and friction (modified from Valle-Levinson, 2008). (c) Idealized gravitational circulation taking into account interactions between bathymetry and friction when rotational effects are negligible. *Source*: Modified from Wong, 1994.

those in the shelf waters with which they exchange water (Alvarez et al., 2006).

Through the Coriolis effect, the Earth's rotation can modify the classical estuarine circulation, whereby the surface net outflow is stronger along the left side of an estuary in the northern hemisphere, looking up-estuary (Fig. 2.8b). Likewise, the net bottom inflow is along the opposite side. The degree to which this occurs depends on how important the Coriolis term is in the overall dynamics of the flow, and thus, this phenomenon is more prominent in higher latitude estuaries that are deep, wide, and stratified (Kasai et al., 2000; Valle-Levinson, 2008). Even under

circumstances when rotational effects are negligible, frictional interactions with bathymetry can strongly influence the pattern of gravitational circulation, where dense inflows occur in the deeper regions of the central channel and surface outflows occur in shallow regions along the shores (Wong, 1994; Fig. 2.8c).

2.6.4 Tidal Circulation

In the absence of river discharge, density gradients, and wind stress, the transport of water in and out of an estuary is driven by tides in response to gravitational interactions between the Sun, Earth, and Moon. Though the tide range varies from one tidal cycle
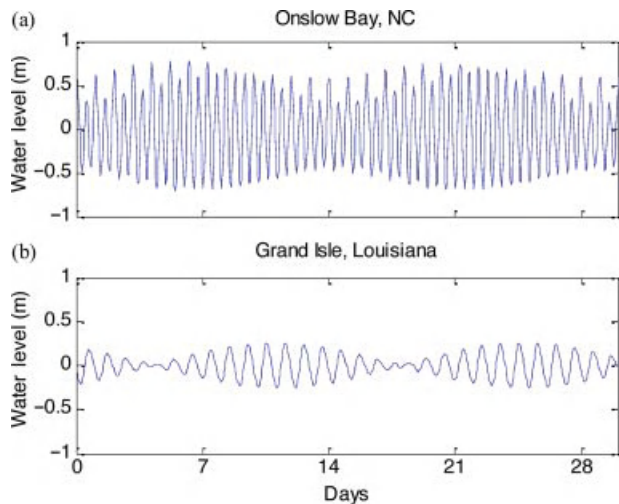
FIGURE 2.9 (a) Semidiurnal tidal water level signal at Onslow Bay, NC, showing spring–neap variability in tide range. (b) Diurnal tidal water level signal at Grand Isle, LA, showing tropic-equatorial variability in tide range.

to the next as the Earth's oceans respond to ever-varying Sun–Moon–Earth configurations, it generally exhibits a fortnightly cycle with maximum and minimum ranges approximately every other week. This cycle is called the *spring–neap cycle* in semidiurnal tidal regimes, and it repeats itself every 14.8 days in response to the relative positioning of the Sun and the Moon (Fig. 2.9a). In diurnal tidal regimes, this fortnightly cycle is called the *tropical–equatorial cycle*, has a period of 13.7 days, and is caused by fortnightly changes in the maximum declination of the Moon's orbit relative to the Earth's equator (Fig. 2.9b).

The rise and fall of water in coastal oceans propagates into estuaries as a long wave. The speed, or celerity, of this wave is reduced by friction at the bottom of the basin or estuary and thus, tidal propagation is slower in shallow water. Because tides take time to progress up an estuarine basin, high tide at the mouth of an estuary may occur much earlier than high tide near the estuary head. The time difference between high tide at the mouth and high tide at some point up-estuary is the *tidal phase lag*.

Though net water transport over a tidal cycle may be close to zero, correlations between velocity and salinity over a tidal cycle can lead to a net transport of salt, typically directed up-estuary, called *tidal pumping*. For example, suppose pure ocean water with salinity 35 psu enters an estuary on an incoming tide. The salt concentration of water leaving the estuary on the ensuing ebb tide will typically be less than 35 psu because the outflowing water will consist of ocean water that entered the estuary on the previous flood tide (35 psu) mixed with relatively fresh estuarine water (<35 psu).

Another process by which tidal currents can lead to net salt transport is through *tidal straining* of the horizontal salinity gradient (Simpson et al., 1990). Tidal straining occurs when there is a vertical shear in the magnitude of the tidal current, brought about by bottom friction, where current velocities near the surface exceed those near the bottom. This shear causes fresher water to flow over more saline water during ebb, enhancing stratification, a process called *strain-induced periodic stratification* (Fig. 2.10). Increasing stratification has the overall effect of stabilizing the water column and restricting turbulent mixing to the dense underlayer, which further enhances the shear. On the flood tide, the opposite happens: stratification is diminished and turbulence is enhanced, which tends to mix the momentum of the two layers, causing a reduction in the vertical current shear (Monismith et al., 1996). Thus, these circumstances can cause the water column to undergo intratidal cycles of stratification and mixing, which can enhance gravitational circulation when the column is stratified or suppress it when the column is mixed.

2.6.5 Wind-Driven Circulation

In addition to circulation driven by tides and density gradients, currents in estuaries can also be driven by wind. Atmospherically forced motions in estuaries are important, because they often are the most significant factors governing the long-term transport and distribution of constituents and can effect volumetric changes between estuaries and their adjacent shelves that are up to an order of magnitude greater than those driven by astronomical tides (Wiseman, 1986).

Numerous studies have shown how estuaries respond to a combination of remote and local effects (Garvine, 1985; Wong, 1991; Wong and Moses-Hall, 1998; Janzen and Wong, 2002; Snedden et al., 2007a). Remote effects occur when winds blowing parallel to the regional coastline immediately outside an estuary cause marked changes in shelf water levels. The water level response on the shelf occurs through the Coriolis effect, where water acceleration in response to wind stress over the surface is directed 90° to the right (left) of the wind direction in the northern (southern) hemisphere, a phenomenon called *Ekman transport*. Thus, in the northern hemisphere, winds blowing to the south will tend to transport water to the west and increase shelf sea levels along a western boundary of an ocean basin (e.g., the Atlantic coast of North America). The increased shelf sea levels produce a pressure gradient between the shelf and adjoining estuaries in the region, ultimately forcing an influx of
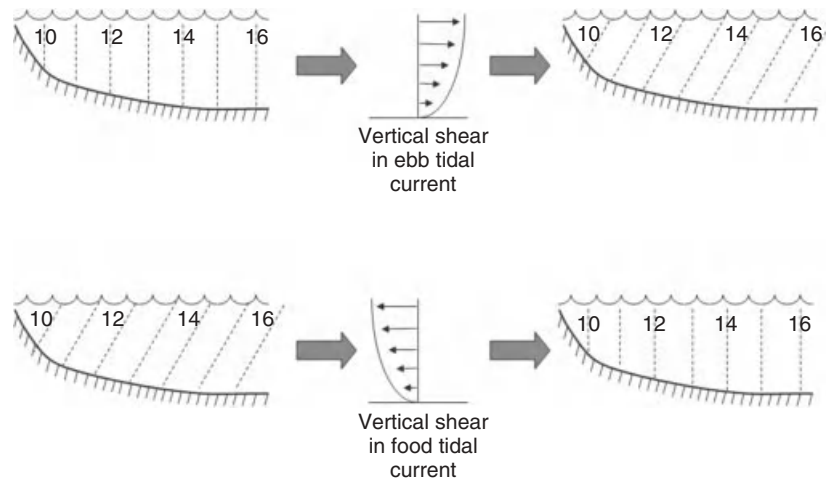
FIGURE 2.10 Changes in stratification brought about by tidal straining. Before onset of ebb tide, stratification is often negligible (upper left). Owing to vertical shear in the tidal current, near-surface waters are advected further seaward than near bottom waters, which increases stratification. The water column then destratifies by the end of the flood tide (lower right).
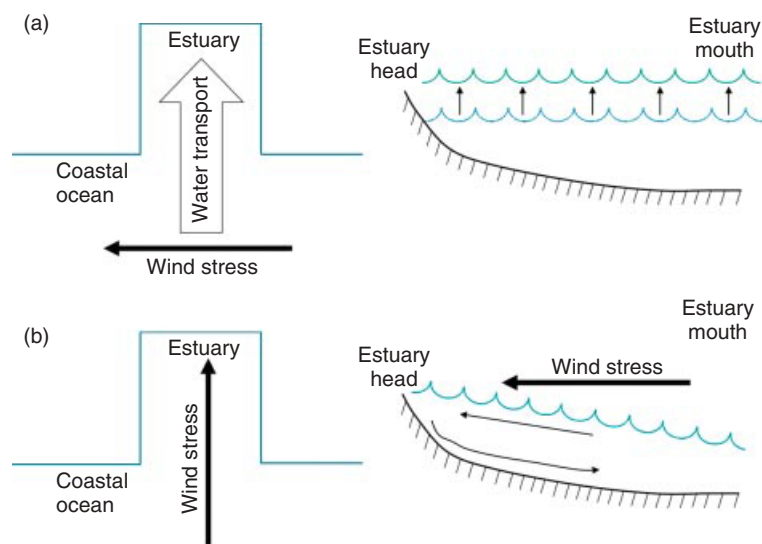
FIGURE 2.11 (a) Remote effect resulting from Ekman transport of shelf waters into an estuary in the northern hemisphere driven by westward winds. Water levels increase throughout the estuary. (b) Local effect resulting from winds blowing landward over the estuary surface. Water levels increase in the landward reaches of the estuary, and currents flow upwind near the surface, and downwind near the bottom.

shelf waters (Fig. 2.11a). The opposite process occurs when winds over the shelf reverse and blow toward the north; shelf waters are transported offshore and coastal sea levels are thus reduced, releasing water from adjoining estuaries onto the shelf. Exchanges forced by this remote mechanism tend to produce flows that are similar in magnitude and direction throughout the water column.

Local effects occur when winds blowing directly over an estuary surface transfer momentum in the atmosphere directly into the upper reaches of the underlying water column and induce a surface current that elevates sea level in the downwind region of the estuary. The resulting sea surface slope within the estuary produces an opposing current in the bottom portion of the water column that is directed upwind (Fig. 2.11b). Because the local effect generates a sea surface slope along the estuary, sea-level responses to this mechanism increase linearly with distance from the estuary mouth. Thus, upper reaches of longer

estuaries, such as Chesapeake Bay, exhibit greater sensitivity to the local effects of wind (Garvine, 1985).

In addition to responding to winds blowing either directly over or immediately outside the estuary, large-scale wind stress fields and moving atmospheric pressure systems can generate very long waves that propagate along the coast. These can be either (i) Kelvin waves, (ii) continental shelf waves, or (iii) coastal trapped waves (Mysak and Hamon, 1969, LeBlond and Mysak, 1978, Gill, 1982), each with their own characteristics (ct., Gill, 1982). These long waves have periods from 2 to 15 days and wavelengths on the order of 1000 km. They travel parallel to the coast, on the continental shelf, at speeds from 0.1 to 1.0 m/s (Brooks and Mooers, 1977). Similar to remotely forced setup, these waves can propagate into estuaries as they move along the regional coastline and facilitate estuary–ocean exchanges that cause substantial changes in estuarine sea levels.

Regardless of the mechanism for wind-forced estuarine motions, their ecological significance can be profound. Exchange flows across estuary-shelf regimes can provide mechanisms for ingress and egress of fish and invertebrates that use estuaries for nursery habitat as juveniles (Pietrafesa and Janowitz, 1988; Tilburg et al., 2005). These exchanges also provide a mechanism for the export of constituents such as carbon (Das et al., 2010). Currents induced by wind forcing also induce changes in estuarine sea levels, the smallest of which can inundate or drain vast tracts of coastal wetlands (Snedden et al., 2007a) and deliver mineral sediments to these landscapes (Snedden et al., 2007b). Wind-forced sea-level fluctuations can also impact plant species composition and productivity through influences on wetland hydroperiod (Baldwin et al., 2001) or soil porewater salinities (Sharpe and Baldwin, 2009).

2.7 ESTUARINE MIXING

2.7.1 Mixing Processes

Estuaries are regions where dense, saline ocean water mixes with waters derived from land drainage. *Mixing* refers to the blending of parcels of water as they move though an estuary in response to ambient currents. As mentioned above, these currents can be driven by freshwater inflows, tides, density gradients, or wind. Mixing is not restricted to water, but also includes dissolved constituents such as salt, nutrients, or pollutants. As such, mixing processes are important determinants to the distribution of constituents within estuaries. Mixing processes can be either *advective* or *dispersive*. Transport of constituents that occurs when they are carried by water flowing through an estuary is called *advection*. When neighboring parcels of water mix together, a net transport of constituents from regions of high concentration to regions of lower concentration can occur. This is *dispersive transport*. The distinction between advection and dispersion is somewhat arbitrary and depends largely on the time frame in question. In general, mixing over longer timescales is considered advection, while over shorter timescales, it is considered dispersion.

Dispersive mixing of water parcels can occur through a variety of processes, including (i) tidal sloshing, (ii) shear effects, (iii) eddy (or turbulent) diffusion, and (iv) molecular diffusion. Introduced in Section 2.6.4, tidal sloshing, which refers to the time-averaged flux of particles by oscillatory tidal currents, is a highly effective dispersive process and has, in fact, been observed to be the dominant dispersive process in many studies (Miranda et al., 1998; Restrepo and Kjerfve, 2002). Generally, dispersion associated with tidal pumping is directed up-estuary.

Shear dispersion results from lateral and/or vertical variability in current velocities that tend to ''smear'' the distribution of constituents throughout an estuary. As an example of lateral shear, if inflowing water on the eastern side of an estuary moves faster than that on the western side, salt will be transported further landward on the eastern side. Similarly, vertical shear dispersion can result in further landward transport of constituents if the velocity of inflowing water near the surface exceeds the velocity near the bed.

Velocity shear also generates turbulent eddies in the water that effectively mix, or disperse, dissolved constituents through turbulent diffusion. The effectiveness of this turbulent mixing in the presence of velocity shear is governed by a property called *eddy viscosity*. It is important to note that eddy viscosity is a property of the flow, not the fluid itself. Turbulence is especially prominent near the bed, where flow over a rough bottom produces turbulent eddies that propagate upward through the water column. Turbulent diffusion can interact with shear to strongly augment dispersion. While dispersion due to molecular diffusion also occurs, it is several orders of magnitude less than turbulent diffusion and is generally considered unimportant (Pond and Pickard, 1983).

Turbulence generated at the bottom boundary also plays a large role in governing the degree of stratification in the water column. The bidirectional flow associated with gravitational circulation acts to induce stratification, and varies in response to

changes in buoyancy forcing, or freshwater discharge into an estuary. On the other hand, tidal currents and the resulting bottom-generated turbulence act to mix the water column, and this mixing power can widely vary throughout the spring–neap cycle. These two opposing forces interact to stratify or mix the water column, depending on which force is more prevalent. Thus, the water column tends to be most stratified during neap tides when buoyancy forcing is strong, and strongly mixed during spring tides when buoyancy forcing is minimal (Haas, 1977; Griffin and LeBlond, 1990; Ribeiro et al., 2004; Miranda et al., 2005). During the mixed state, nutrients and food particles in the bottom layer can mix up into the photic surface zone and enhance production and, in addition, force oxygen-rich surface waters to the bottom, replenishing oxygen (Nezlin et al., 2009). Because tidal stirring power is an exponential function of velocity (Simpson et al., 1990), even relatively small changes in tidal current amplitude can have large impacts on stratification.

Though tidal forcing is usually the most important cause of mixing in estuaries, turbulence induced by wind stress across an estuary surface can also govern stratification (Goodrich et al., 1987; Van de Kreeke and Robaczewska, 1989). Direct wind mixing is usually of lesser importance in estuaries unless the tidal range is small or the estuary consists of large open areas or is shallow, as in the case of many lagoons. The wind is usually responsible for the generation of surface waves, internal waves (Leder, 2002), basin seiches (Luettich et al., 2002), and Langmuir wind rows/cells. Each of these wave types at times enhances mixing in estuaries significantly.

In addition to generation at the bottom boundary layer through bottom friction or at the surface by wind stress, turbulence can also be generated within the water column near the pycnocline. Stratification in this region tends to confine turbulent mixing to the lower layer, which further enhances stratification. The strong density discontinuity promotes vertical shear between the two layers, and as the shear becomes large relative to the degree of stratification, turbulence develops internally, allowing for mixing throughout the stratified water column (Peters, 1997).

2.7.2 Mixing Diagrams

As a dissolved or suspended constituent is transported into an estuarine region, it is subjected to advective and dispersive mixing processes as well as changes in salinity. The end result is often that various constituents will settle out within the estuary, making the system act as a material sink. This is largely the case with fine-grained sediments from river sources

as well as sand-sized sediments from the coastal ocean (Meade, 1969). Thus, an important question to ask is whether a dissolved or suspended constituent mixes conservatively within the estuary versus whether it is added to or subtracted from the water column. It would mix conservatively if the material concentration changes proportionately to the change in salinity. Salinity is a conservative constituent, and if a material concentration is plotted linearly against salinity, it too would be conservative. Such a plot of salinity against a material concentration is referred to as a *mixing diagram*. Systematic deviation of a measured estuarine concentration from a straight line in a mixing diagram is interpreted to imply nonconservative behavior of the constituent. This would then usually imply that the estuary is a sink or a source for a given constituent.

However, extreme care must be exercised in using a mixing diagram. The transformation from distance along an estuary to salinity assumes (i) one-dimensional (longitudinal) mixing, (ii) quasi-steady state, and (iii) that all data are averaged over one or more complete tidal cycles (Officer, 1979; Officer and Lynch, 1981; Loder and Reichard, 1981). Applications of the constituent–salinity mixing diagram approach require that all transformations affecting the constituent in the estuary occur at a rate slower than the rate of estuarine flushing, as shown analytically by Boyle et al. (1974). These assumptions are seldom met in the strict sense, and thus deviations from a straight line in a mixing diagram may not necessarily mean nonconservative behavior. In particular, it is well known (Loder and Reichard, 1981; Officer and Lynch, 1981) that temporal variations in either the riverine or oceanic material concentrations can cause nonlinear mixing curves in spite of a constituent behaving conservatively. Corrections can be made, with difficulty, for this problem if sufficient data are available. The idea of mixing diagrams is developed further in Chapter 3.

2.7.3 Dynamic Classification

Rather that classifying estuaries according to geomorphic characteristics, Pritchard (1955) proposed a useful classification scheme based on circulation and stratification. The three basic estuarine types are A (highly stratified), B (partially mixed), and C (well mixed). The C type may be subdivided into C1 (vertically homogeneous with laterally reversing net flow) and C2 (vertically and laterally homogeneous).

The highly stratified type A estuary is exemplified by the lower Mississippi River. The density (or salinity) stratification is extremely sharp, so that pure fresh and pure salt water are virtually adjacent, and vertical

salt exchange occurs as a function of the breaking of internal waves along the mid-depth pycnocline. The type A estuary usually exhibits a low tidal range, which cannot break down the vertical stratification, and a moderate to great amount of freshwater input.

The partially mixed estuary, type B, is exemplified by the Chesapeake Bay estuarine system. The vertical salt gradient has the shape of the cotangent curve with time-averaged salinity differences from 2 to 10 ppt between surface and bottom waters. The classical estuarine circulation (i.e., a well-developed gravitational circulation) is typical for type B systems, which for the most part are coastal plain estuaries or fjärd or shallow fjord system. These systems are characterized by moderate to large tidal ranges and moderate freshwater inflow.

The well-mixed estuary, type C, is exemplified by North Inlet, South Carolina. Tidal mixing is intense because of a large tidal range and little freshwater influx. Accordingly, there are no vertical density (or salinity) gradients. The net circulation is either everywhere seaward (C2) or with one side flowing in and the other side flowing seaward in cross section. In the latter case, tidal pumping is the dominant circulation mode.

An estuary's classification need not be static. Changes in stratification brought about by variations in tidal stirring power (e.g., the spring–neap cycle) or buoyancy forcing can affect changes in an estuary's classification. For example, Miranda et al. (1998) found that Brazil's Bertioga Channel is a type A estuary (highly stratified) during neap tides but transitions to a type B or C estuary (partially mixed or well mixed, respectively) during spring tides. Anthropogenic impacts may also influence an estuary's classification. Pritchard (1955) suggested that in managing estuaries, it would be possible to change the circulation and mixing characteristics of a particular estuary from A toward C or from C toward A. By dredging an estuary and thus making it deeper, the estuary can be expected to alter its characteristics from A to B or B to C. Similarly, by widening a channel, the characteristics of that section can be expected to change toward a B or a C type if all other parameters are held constant. The damming of rivers leading into an estuary can likewise change the estuarine dynamics because of the change in buoyant mixing. The greater the discharge, the more likely is the A-type estuary because of a well-developed vertical stratification. With decreasing river input the type A may become a type B, and the type B a type C.

2.7.4 Circulation–Stratification Diagram

Hansen and Rattray (1966) proposed an improvement on the dynamical classification of estuaries by a dimensionless circulation–stratification diagram (Fig. 2.12). By plotting a stratification parameter versus a circulation parameter, they managed to describe a continuum of estuaries and show how a given estuary may change over a season.

The stratification parameter is simply the ratio of the salinity difference between bottom and surface layers and the depth-averaged salinity. Each of these salinities is first averaged over one or more complete tidal cycles. The circulation parameter is likewise a ratio between the net surface flow and the freshwater flow. The net surface flow is taken as a representative value across an estuarine section to smooth out lateral effects and with the assumption of a steady state. Thus, changes in water level from beginning to end of a tidal cycle are averaged out. The freshwater flow is simply the steady freshwater discharge divided by the cross-sectional area.

Hansen and Rattray (1966) found that most estuaries could be grouped into four regions on their diagram. Class 1 estuaries are either lagoons or bar-built estuaries. Class 1a is vertically mixed and includes North Inlet, whereas 1b exhibits more vertical stratification. Both, however, have a total lack of gravitational circulation. Upstream salt mixing takes
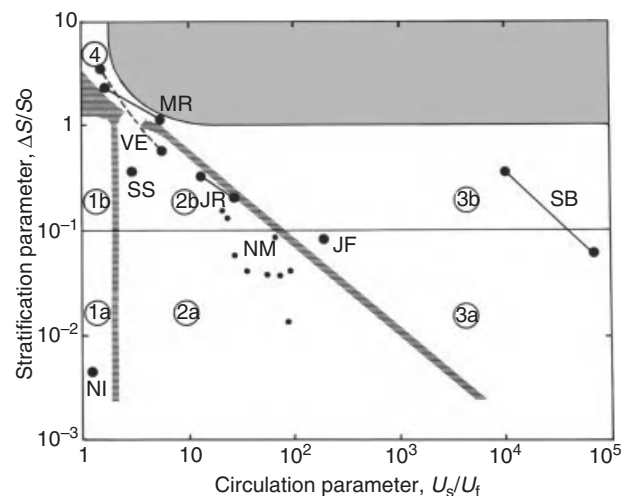
FIGURE 2.12 Estuarine classification diagram (Hansen and Rattray, 1966) according to nondimensional stratification and circulation parameters. MR, Mississippi River; VE, Vellar Estuary, India; NI, North Inlet, SC; SS, South Santee, SC; JR, James River, VA; NM, Narrows of Mersey, UK; JF, Straits of Juan de Fuca, WA; and SB, Silver Bay, AK. *Source*: Copyright 1966 by the Association for the Sciences of Limnology and Oceanography, Inc. Used with permission.

place by longitudinal dispersion mechanisms alone. Most estuaries studied fall into class 2, which overlaps with coastal plain and partially mixed estuaries. Again, this type was subdivided into a well-mixed (2a) and a weakly stratified (2b) subclass. This class is characterized by reasonably well-developed gravitational circulation and longitudinal mixing by both dispersive and advective mechanisms.

Class 3 estuaries, on the other hand, are dominated by advective mixing processes, with dispersive effects playing a negligible role. Most systems in this class show moderate to strong stratification and are further characterized by well-developed gravitational circulation. This class includes most fjärd and some fjord estuaries and a number of estuarine straits.

Class 4 estuaries, finally, coincide with Pritchard's (1955) type A, the strongly stratified system. Vertical mixing is limited and the gravitational circulation is weak or nonexistent.

Hansen and Rattray's (1966) classification represents an improvement over previous classification schemes in that it allows a direct comparison of estuarine dynamics and mixing processes between systems. This, in turn, makes it possible to generalize to some degree about different estuaries. With this basic background in the physics of estuaries, it is now possible to consider the chemistry and biology of estuaries, which are very much influenced by these basic physical properties.

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CHAPTER THREE

ESTUARINE CHEMISTRY

Thomas S. Bianchi

3.1 BASICS IN BIOGEOCHEMICAL CYCLES AND CHEMICAL PRINCIPLES

3.1.1 Global Biogeochemistry

Some of the first applications of the integrative field of Biogeochemistry are derived from organic geochemical studies where organisms and their molecular biochemistry were used as an initial framework for interpreting sources of sedimentary organic matter (SOM; Abelson and Hoering, 1960; Eglinton and Calvin, 1967). Biogeochemical cycles involve the interaction of biological, chemical, and geological processes that determine sources, sinks, and fluxes of elements through different reservoirs within ecosystems (Bianchi, 2007). For example, a *reservoir* is the amount of material (M), as defined by its chemical, physical, and/or biological properties. The units used to quantify material in a reservoir, in the box or compartment of a box-model, are typically mass or moles. *Flux* (F) is defined as the amount of material that is transported from one reservoir to another over a particular time period (mass/time or mass/area/time). A *source* (S_i) is defined as the flux of material *into* a reservoir, whereas a *sink* (S_o) is the flux of material *out* of the reservoir (many times proportional to the size of the reservoir). The *turnover time* is required to remove all the materials in a reservoir, or the average time that elements spend in a reservoir. Finally, a *budget* is essentially a ''checks and balances'' of all the sources and sinks as they relate to the material turnover in reservoirs (Chapter 17). For example, if the sources and sinks are the same, and do not change over time, the reservoir is considered to be in a *steady state*. The term *cycle* refers to when there are two or more connecting reservoirs, whereby materials are cycled through the system—generally with a predictable pattern of cyclic flow.

The spatial and temporal scales of biogeochemical cycles vary considerably depending on the reservoirs considered. In the case of estuaries, most biogeochemical cycles are based on regional rather than global scales. However, with an increasing awareness of the importance of atmospheric fluxes of biogases (e.g., CO_2, CH_4, and N_2O) in estuaries and their impact on global budgets (Seitzinger, 2000; Frankignoulle and Middelburg, 2002), some budgets will involve both regional and global scales.

3.1.2 Thermodynamics and Kinetics

Before discussing the chemical dynamics of estuarine systems, it is important to briefly review some of the basic principles of *thermodynamic* or *equilibrium models* and *kinetics* that are relevant to upcoming discussions in aquatic chemistry. Similarly, the fundamental properties of freshwater and seawater are discussed because of the importance of salinity gradients and their effects on estuarine chemistry.

Owing to the complexity of natural systems, equilibrium models can tell you something about the

chemical constituents (gases, dissolved species, and solids) under well-constrained conditions (no change over time, fixed temperature, pressure, and homogeneous distribution of constituents). Equilibrium models will tell you something about the chemistry of the system at equilibrium but will not tell you anything about the kinetics with which the system reached equilibrium state. The laws of thermodynamics are the foundation for chemical systems at equilibrium. The basic objectives in using equilibrium models in estuarine/aquatic chemistry is to calculate equilibrium compositions in natural waters, to determine the amount of energy needed to make certain reactions occur, and to ascertain how far a system may be from equilibrium. For more details on this, the reader is referred to the study by Stumm and Morgan (1996).

Chemical kinetic models provide information on reaction rates that cannot otherwise be obtained in chemical thermodynamics (Bianchi, 2007). However, in many situations, information, such as kinetic rate constants, needed for such models are not available. The basic premise in kinetics is to relate the rate of a process to the concentration of reactants. For example, we can examine the formation and dissociation of species AB as it relates to reactants A and B in the following reactions:

$$k_a \quad k_b$$
$$A + B \rightarrow AB \text{ and } AB \rightarrow A + B \quad (3.1)$$
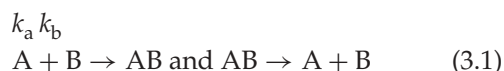
where k_a is the rate constant of formation and k_b, the rate constant of dissociation.

The units of the rate constants (e.g., seconds and days) will depend on the units of concentrations as well as the exponents. Temperature is another important factor that is critical in affecting rate constants. It is well established that temperature increases chemical reaction rates and biological processes—particularly important in estuarine, biogeochemical cycles are the effects on microbial reactions. The following well-known equation used to describe these effects is referred to as the *Arrhenius equation*:

$$k = Ae^{-E_a/RT} \quad (3.2)$$

where k is the rate constant, A, the frequency factor (number of significant collisions producing a reaction), E_a, the *activation energy* (amount of energy required to start a reaction, in J), R, the *universal gas constant* $= 0.082057$ dm^3 atm/mol/K, and T, the *absolute temperature* (K).

The rates of chemical processes usually increase in the range of 1.5–3.0, and biological processes by a factor of 2.0, for a $10°C$ increase (Brezonik, 1994).

The most common way, not necessarily the best, of dealing with the temperature dependence of biological processes began with a study on fermentation rates (Berthelot, 1862), where it was suggested that since rate increases with temperature, k at $T + 1$ is greater than k at $T - 1$ by a fixed proportion. It has become common to use a ratio over a $10°$ difference, or what is called the Q_{10} defined as follows:

$$Q_{10} = \frac{k(T + 10)}{k(T)} \quad (3.3)$$

Because log k does not go up linearly with temperature, Q_{10} will be dependent on the temperatures of comparison. The larger the Q_{10}, the greater the effect temperature has on the reaction. A value of $Q_{10} = 1$ implies that temperature has no effect on the reaction. Consequently, many of the global biogeochemical cycles mediated by biological processes are highly dependent on temperature, perhaps most notably trace gas (e.g., CO_2 and CH_4) cycles—as they relate to global warming. Other factors involved in controlling the chemical kinetics of reactions might include catalytic reactions, kinetic isotope effects, and enzyme-catalyzed reactions (Butcher and Anthony, 2000).

If we consider the dissolution of a simple mineral salt such as NaCl where the ions are efficiently hydrated by water molecules, the ion interactions between Na^+ and Cl^- are essentially insignificant, as well as with H^+ and OH^-. Conversely, the solubility of other mineral salts may be enhanced with the formation of ion pairs (Millero, 1996), a *salting-in effect*, requiring the inclusion of ion speciation effects (Pankow, 1991). In contrast, there is commonly a *salting-out effect* of dissolved constituents across a salinity gradient; this can be particularly important when examining more hydrophobic organic compounds, such as aromatic hydrocarbons in estuaries (Means, 1995). Certainly, with any calculation under equilibrium conditions, solubility of these mineral salts is a function of temperature, pressure, and ionic strength. Thus, effects of changing salinity gradients in estuarine environments will have a dramatic effect on the solubility of minerals.

3.1.3 Redox Chemistry

The significant oxygen gradients commonly found in estuarine waters and surface sediments is largely controlled by stratification, which is a function of tidal and wind mixing, and organic matter loading (Officer et al., 1984; Borsuk et al., 2001; Bianchi, 2007). Consequently, redox and acid–base reactions are also important in determining the state of an ion in

estuarine waters. The half-reactions typically used to describe reduction/oxidation (*redox*) are as follows:

$$OX_1 + ne^- = RED_1 \text{ half-reaction 1} \qquad (3.4)$$

$$RED_2 = OX_2 + ne^- \text{ half-reaction 2} \qquad (3.5)$$

where OX is the oxidized form, RED, the reduced form, and n, the number of electrons (e^-) transferred. When combined, the half-reactions and the final redox equation are as follows:

$$OX_1 + RED_2 = RED_1 + OX_2 \qquad (3.6)$$

This equation represents the exchange of electrons between OX_1 and RED_2 to produce RED_1 and OX_2. In this, OX_1 is considered to be the *oxidant* because it oxidizes RED_2 to OX_2, and RED is the *reductant* because it reduces OX_1 to RED_1. A typical redox half-reaction that occurs in estuarine waters is the reduction of Fe^{3+} to Fe^{2+}:

$$Fe^{3+} + e^- = Fe^{2+} \qquad (3.7)$$
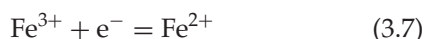
Redox in sediments is typically defined by E_h (redox potential) where positive values indicate oxidizing conditions (Stumm and Morgan, 1996). In redox chemistry, the half-reaction concept is used to understand E_h, which is the electron activity in volts relative to a standard hydrogen electrode (Chester, 2003). Thus, the activity of electrons in solution is expressed by electron activity ($p\varepsilon$), a dimensionless term, or E_h (volts) by the following equation:

$$p\varepsilon = \frac{F}{2.3RT}(E_h) \qquad (3.8)$$

where F is the Faraday's constant, R, the gas constant, and T, the absolute temperature. E_h conditions are primarily controlled by production and decomposition of organic matter; positive values are oxidizing and negative values are reflective of reducing conditions (Fig. 3.1; Bianchi, 2007). The depth of the *redox potential discontinuity* (RPD) layer is associated with distinct coloration, indicative of differences between oxic and suboxic conditions (Fenchel and Riedl, 1970; Santschi et al., 1990). The oxidized region in surface sediments of estuarine sediments (one to a few centimeters of sediment) is typically orange-brown (*Fe* and *Mn oxides*) followed by a reduced region that is gray-black (*mono- and polysulfides*). The depth of the RPD is largely controlled by the amount of organic matter loading, physical mixing, and bioturbation.
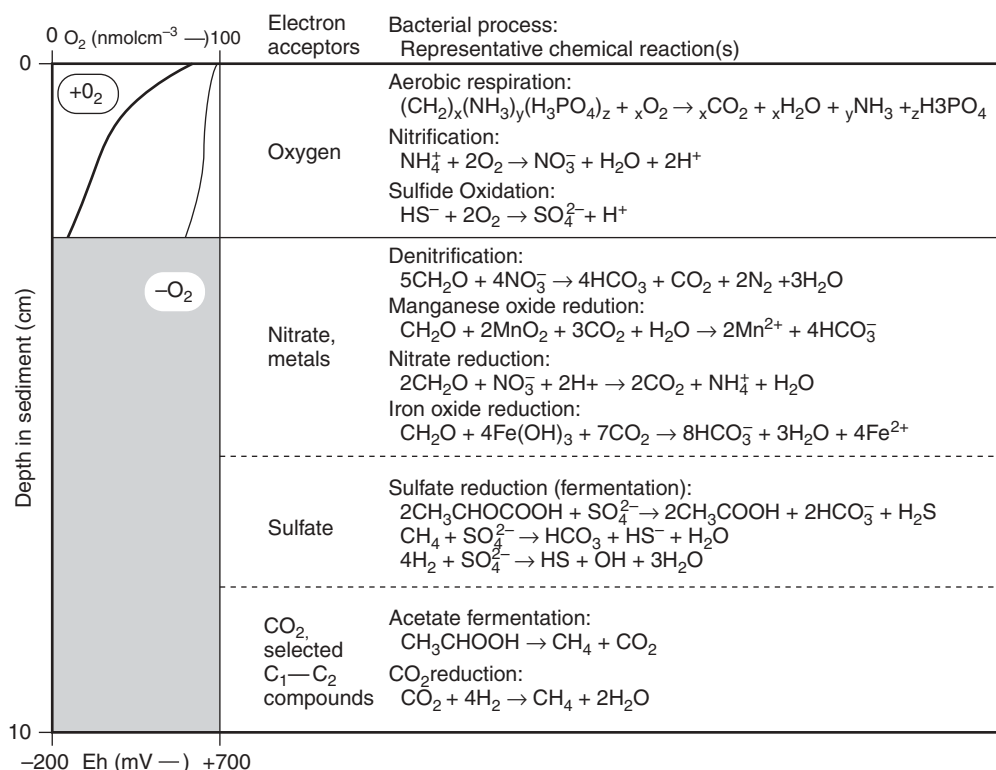
FIGURE 3.1 Bacterial decomposition of organic matter in marine/estuarine sediments through a sequence of terminal electron acceptors (e.g., O_2, NO_3^-, MnO_2, FeOOH, SO_4^-, and CO_2) and changing redox. *Source:* Modified from Deming and Baross (1993).

Recent work has shown that the location of the RPD depth is very similar when measured by electrodes in sediment cores or sediment profile images (Rosenberg et al., 2001).

The decomposition of organic matter in marine/ estuarine sediments proceeds through a sequence of *terminal electron acceptors* (e.g., O_2, NO_3^-, MnO_2, $FeOOH$, SO_4^-, and CO_2; Froelich et al., 1979; Canfield, 1993) as shown in Figure 3.1 (Deming and Baross, 1993). The sequence of reactions is principally determined by the free energy yields (ΔG^0) of per mole of organic C. In essence, the products of one electron acceptor become the electron donor for another electron acceptor such as the oxidation of Fe^{2+} and FeS by MnO_2 and NO_3^-. While this sequence provides a basic framework from which to work, recent work has shown that the versatility of many bacteria may allow for several of these reactions to occur in the same zone (Brandes and Devol, 1995).

3.2 MIXING AND PARTICLE EFFECTS ON CHEMISTRY OF ESTUARINE WATERS

3.2.1 Reactivity of Dissolved Constituents

The mixing of river water and seawater can be quite varied in different estuarine systems resulting in a water column that can be highly or weakly stratified/mixed (Bianchi, 2007). These intense mixing and ionic strength gradients can significantly affect concentrations of both dissolved and particulate constituents in the water column through processes such as *sorption/desorption and flocculation*, as well as biological processes. The reactivity of a particular estuarine constituent has been traditionally interpreted by plotting its concentration across a conservative salinity gradient. As shown by Wen et al. (1999), the simplest distribution pattern, in a one-dimensional, two end-member, steady-state system, would be for a *conservative constituent* to change linearly with salinity (Fig. 3.2; Bianchi, 2007). For a *nonconservative constituent*, when there is net loss or gain in concentration across a salinity gradient, extrapolation from high salinities can yield an ''effective'' river concentration (C^*). This ''effective'' concentration can be used to infer reactivity of a constituent and can be used to determine total flux of the constituent to the ocean. For example, when $C^* = C_0$, the constituent is behaving conservatively, when $C^* > C_0$, there is removal of the constituent (nonconservative behavior) within the estuary, and when $C^* < C_0$, the constituent is
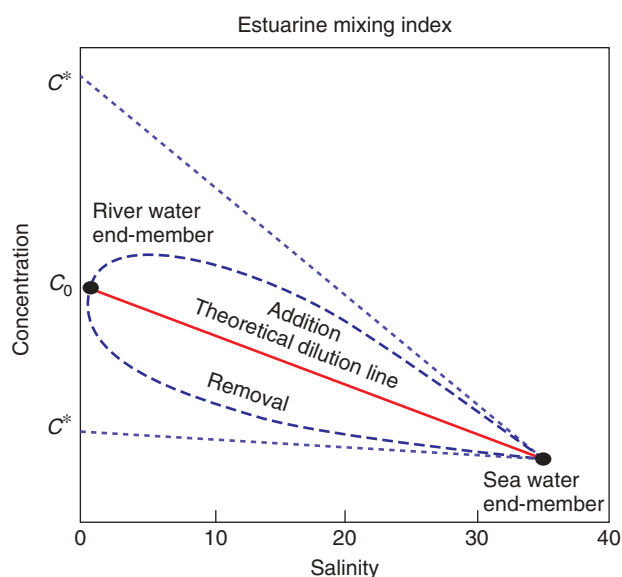
FIGURE 3.2 Illustration of the simplest distribution pattern, in a one-dimensional, two end-member, steady-state system for a conservative constituent to change linearly with salinity. *Source:* From Wen et al. (1999).

being added (nonconservative behavior) within the estuary. River flux (F_{riv}) to the estuary and ultimately to the ocean is commonly estimated using this simplified mixing model. The flux of material into an estuary is $F_{riv} = RC_0$, where R is the river water flux. Similarly, flux from the estuary to the ocean (F_{ocean}) can be estimated by $F_{ocean} = RC^*$. Finally, the overall net internal flux (F_{int}) from input or removal can be estimated by $F_{int} = R(C^* - C_0)$.

Despite widespread application of the standard mixing model in estuarine systems, there are numerous problems when invoking these simple steady-state mixing assumptions. Early work showed that nonreactive constituents can display nonconservative mixing due to timescale differences in river concentrations of the constituent relative to estuarine mixing timescales (Officer and Lynch, 1981).

The relative importance of fluxes of dissolved constituents from groundwater inputs to estuarine and shelf waters is yet another transport mechanism that adds complexity to the estuarine mixing index. Groundwater inputs of nutrients to estuaries can be quite considerable (Kelly and Moran, 2002) enhancing the nonconservative behavior of nutrients.

## 3.2.2 Effects of Suspended Particulates and Chemical Interactions

Particulates in estuarine systems are composed of both *seston* (discrete biological particles) and

inorganic lithogenic components. An operational cutoff definition of 0.45 μm is used in this section to discriminate particulates. The highly dynamic character of estuarine systems (e.g., tides, wind, and resuspension) can result in considerable variability in particle concentration over diurnal time intervals (Fain et al., 2001). Moreover, the reactivity of these particles can change over short spatial intervals due to rapid changes in salinity, pH, and redox conditions (Herman and Heip, 1999). Water column particulates in estuaries, primarily derived from rivers, adjacent wetland systems, and resuspension events, are important in controlling the fate and transport of chemicals in estuaries (Turner and Millward, 2002). A recent review by Turner and Millward (2002), with particular emphasis on metals and hydrophobic organic micropollutants, showed that processes such as ion exchange, adsorption–desorption, and precipitation–dissolution were critical in controlling the partitioning of chemical species in estuaries (Fig. 3.3). Biological processing of particulates by both pelagic and benthic micro- and macroheterotrophs is also critical in estuaries.

Lithogenic particles are derived from weathering of crustal materials and mostly comprise the primary minerals quartz, feldspar, secondary silicate minerals such as clays, and hydrogenous components (Fe and Mn oxides, sulfides, and humic aggregates) formed *in situ* by chemical processes (Turner and Millward, 2002). Mineral surfaces on these particles are important in binding organic molecules, gels, and microaggregates (Mayer, 1994a,b; Aufdenkampe et al., 2001). The fate of organic molecules in estuarine systems largely depends on whether they are sorbed to mineral surfaces (Keil et al., 1994a,b; Baldock and Skjemstad, 2000). For example, selective partitioning of basic amino acids (positively charged) to clay particles (negatively charged) has significant effects on the composition of dissolved amino acids in river waters of the Amazon Basin (Aufdenkampe et al., 2001). Similarly, concentrations of many trace metals in estuarine waters are also influenced by sorption–desorption interactions with suspended particles (Santschi et al., 1999).

Biogenic particulates derived from fecal pellets and planktonic and terrestrial detrital materials are also important in controlling chemical interactions in estuaries (Bianchi, 2007). Other suspended particulates composed of complex aggregates of biogenic and lithogenic materials have similar effects. Many of these biogenic particles are degraded and converted to dissolved organic matter (DOM), which can then be sorbed to lithogenic particles providing an organic coating. These organic coatings are important in controlling the surface chemistry of particulates in aquatic environments (Loder and Liss, 1985; Wang and Lee, 1993). Organic detrital particulates also affect the adsorption of amines (Wang and Lee, 1990) and ammonium (Mackin and Aller, 1984) in sediments.
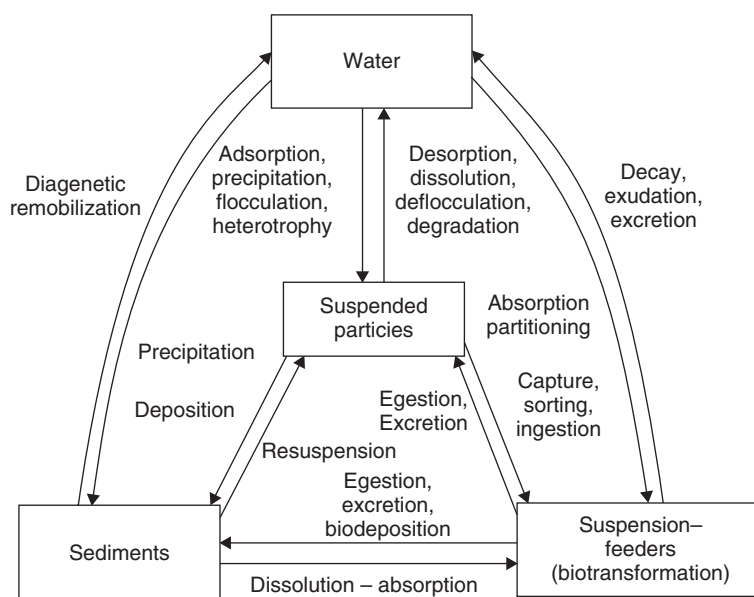

FIGURE 3.3 Processes critical in controlling the partitioning of chemical species in estuaries with particular emphasis on metals and hydrophobic organic micropollutants (HOMs). *Source:* Modified from Turner and Millward (2002).

3.2.3 Sources and Mixing of Dissolved Salts in Estuaries

Before discussing the factors that control concentrations of the major dissolved components in rivers, estuaries, and oceans, it is important to discuss the operationally defined size-spectrum for different phases (dissolved, colloidal, and particulate) of an element. The conventional definition for dissolved materials is the fraction of total material that passes through a membrane filter with a nominal pore size of 0.45 μm (Fig. 3.4; Wen et al., 1999). Although ultrafilters are available for isolation of colloidal materials, this fraction is traditionally included within the dissolved fraction. However, *colloids* are not considered to be truly dissolved even though some of them pass through a 0.45-μm filter.

All natural waters in the world have a certain amount of salts dissolved in them. From a chemical perspective, estuarine environments are places where seawater is measurably diluted by freshwater inputs from the surrounding drainage basin. The mixing of river water and seawater in estuarine basins is highly variable and typically characterized by sharp concentration gradients. In simple terms, estuaries contain a broad spectrum of mixing regimes between two dominant end-members—rivers and oceans. Rivers have highly variable amounts of salts in them typically ranging in a few hundreds of milligrams per liter, whereas the oceans have more stable concentrations in the range of grams per liter.

The sources of salts in rivers are primarily derived from the weathering of rocks in the drainage basin of rivers and estuaries, in addition to other human activities (e.g., agriculture; Burton and Liss, 1976; Berner and Berner, 1996; Bianchi, 2007). When examining the relationship between drainage basin area and total sediment discharge in major rivers of the world, it becomes clear that factors other than basin area are important. In addition to basin area, other factors typically include the following: relief (elevation) of the basin, amount of water discharge, influence of lakes/dams (e.g., storage) along river, geology of basin, and climate (Milliman, 1980; Milliman and Syvitski, 1992). Consequently, the composition of suspended materials in rivers is largely a function of the soil composition of the drainage basin. However, significant differences exist between the chemical composition of suspended materials in rivers and the parent rock material. This is due to differences in the solubility of different elements in parent rock materials. For example, elements such as Fe and Al are less soluble than Na and Cl, making them less abundant in the dissolved materials and more abundant in the suspended load of rivers, respectively (Berner and Berner, 1996). This enrichment of Fe and Al is further supported by the element weight ratio, which if >1 indicates elemental enrichment. In some cases, rivers may receive the majority of salt inputs through precipitation and evaporation processes. This relationship was established when Gibbs (1970) plotted
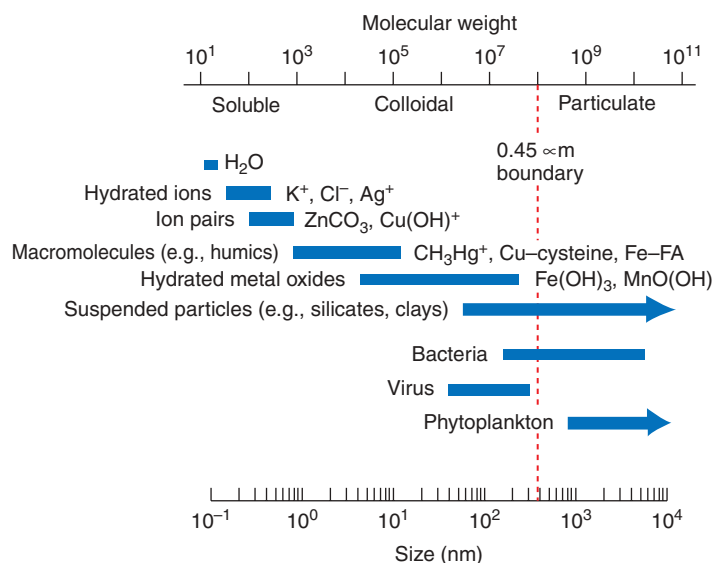
FIGURE 3.4 Conventional definition for dissolved materials shown as the fraction of total material that passes through a membrane filter with a nominal pore size of 0.45 μm. *Source:* From Wen et al. (1999).

the total dissolved solids concentration of rivers versus the compositional indices of $Na^+/(Na^+ + Ca^{2+})$ and $Cl^-/(Cl^- + HCO_3^-)$).

A historical account of measurements of major dissolved components of seawater indicates that the most abundant elements, in order of decreasing abundance are Cl^-, Na^+, Mg^{2+}, SO_4^{2-}, Ca^{2+}, and K^+ (Table 3.1; Millero, 1996). In contrast to rivers, the major constituents of seawater are found in relatively constant proportions in the oceans, indicating that the residence times of these elements are long (thousand to millions of years)—highly indicative of nonreactive behavior (Millero, 1996). This relative constancy of major (and many minor) elements in seawater is referred to as the *rule of constant proportions or Marcet's principle*. More specifically, these elements are considered to be *conservative elements*, whereby changes in the concentrations of these elements reflect the addition or loss of water through physical processes. While these elements may be involved in other chemical or biological reactions, concentration changes from these processes are too small to change the constancy of the elemental ratios (Wangersky and Wangersky, 1980; Libes, 1992). The remaining elements in seawater are termed *nonconservative* because they do not remain in constant proportion due to biological (e.g., uptake via photosynthesis) or chemical (e.g., hydrothermal vent inputs) processes. In estuaries, as well as other oceanic environments (e.g., anoxic basins, hydrothermal vents, and evaporated basins), the major components of seawater can be altered quite dramatically due to numerous processes (e.g., precipitation, evaporation, freezing, dissolution, and oxidation).

TABLE 3.1 **Relative composition of major components of seawater ($pH_{sws} = 8.1$, $S = 35$, and $25°C$)**

Solute	$g_i/Cl(‰)$
Na^+	0.55661
Mg^{2+}	0.06626
Ca^{2+}	0.02127
K^+	0.02060
Sr^{2+}	0.00041
Cl^-	0.99891
SO_4^{2-}	0.14000
HCO_3^-	0.00552
Br^-	0.00347
CO_3^{2-}	0.00083
$B(OH)_4^-$	0.000415
F^-	0.000067
$B(OH)_3$	0.001002
Σ	1.81540

Source: Modified from Millero (1996).

3.2.4 Measurement of Salinity

Salinity was first rigorously defined by Knudsen (1902) as "the weight in grams of the dissolved inorganic matter in one kilogram of seawater after all bromide and iodide have been replaced by the equivalent amount of chloride and all carbonate converted to oxide." The relative constancy of the major ions in seawater is constant enough that determination of one major component could be used to determine the other components in a sample.

Owing to the accuracy and reproducibility of the measurement, chloride was chosen as the ion of choice. Libes (1992) defines *chlorinity* as "the mass in grams of halides (expressed as chloride ions) that can be precipitated from 1000 g of seawater by Ag^+." This is referred to as the *Mohr titration*, where silver nitrate is used to titrate seawater with potassium chromate as an indicator. Chlorinity can also be estimated using density and conductivity measurements (Cox et al., 1967). Thus, salinity is now commonly measured using an inductive *salinometer*, where the conductivity of water is measured; in essence, the electrical current is controlled by the movement and abundance of ions; the more the dissolved salts, the greater the conductivity. Since much of the earlier work was presented in terms of salinity and chlorinity, the two units are related, by definition, according to the following equation:

$$S(‰) = 1.80655 \, Cl(‰) \tag{3.9}$$

3.2.5 Dissolved Gases and Atmosphere–Water Exchange

Dissolved gases are critically important in many of the biogeochemical cycles of estuaries and coastal waters (Bianchi, 2007). However, only recently have large-scale collaborative efforts addressed the importance of air–water exchange in estuaries. For example, the Biogas Transfer in Estuaries (BIOGEST) project, which began in 1996, was focused on determining the distribution of biogases (CO_2, CH_4, carbon monoxide (CO), nonmethane hydrocarbons, N_2O, dimethylsulfide [DMS], carbonyl sulfide (COS), volatile halogenated organic compounds, and some biogenic volatile metals) in European estuaries and their impact on global budgets (Frankignoulle and Middelburg, 2002). The role of estuaries and other coastal ocean environments as global sources and/or sinks of key greenhouse gases, such as CO_2, has also been a subject of intense interest in recent years (Raymond et al., 1997, 2000; Cai, 2003; Wang and Cai, 2004). Similarly, O_2 transfer across the air–water interface is critical for the survival of most aquatic

organisms. Unfortunately, many estuaries around the world are currently undergoing eutrophication, which commonly results in low O_2 concentrations (or *hypoxic = < 2 mg/l*), due to microbial respiration of organic matter produced by phytoplankton responding to excessive nutrient loading in these systems (Rabalais and Turner, 2001; Rabalais and Nixon, 2002).

To understand how gases are transferred across the air–water boundary, the dominant atmospheric gases and physical parameters that control their transport and solubility in natural waters are first examined. The atmosphere is also composed of *aerosols*, which are defined as condensed phases of solid or liquid particles, suspended in state, that have stability to gravitational separation over a period of observation (Charlson, 2000). Chemical composition and speciation in atmospheric aerosols is important to understand their behavior after deposition and is strongly linked with the dominant sources of aerosols (e.g., windblown dust, sea salt, and combustion). The importance of aerosol deposition on estuaries and coastal waters, via precipitation (rain and snow) and/or dry particle deposition, has received considerable attention in recent years. For example, *dry and wet deposition* of nutrients (Paerl et al., 2002; Pollman et al., 2002) and metal contaminants (Siefert et al., 1998; Guentzel et al., 2001) has proven to be significant in biogeochemical budgets in wetlands and estuaries.

The direction in exchange of gases across the air–water interface will change accordingly as atmospheric and aqueous concentrations of respective gases change over time. When rates of exchange for a particular gas are equal across the air–water interface, the gas is considered to be in *equilibrium*; this is when the concentration of the gas in both aqueous (P_A) and gas phases (P_i) are equal. The equilibrium concentration of a gas in the aqueous phase is directly proportional to the pressure of that gas—this is referred to as *Henry's law of equilibrium distribution*, as defined by the following equation:

$$P_A = K_H P_i \qquad (3.10)$$

where K_H is Henry's law constant and P_A, the concentration of gas in the aqueous phase (expressed as mol/kg).

The solubility of gases is influenced by their molecular weight. In general, the heavier the molecule, the greater is its solubility, excluding cases where there are molecules that interact more strongly with water. Over a range of temperatures, the solubilities of N_2, O_2, Ar, Ne, and He in seawater at salinity 35, 1 atm, and 100% humidity are seen (Table 3.2). It becomes apparent that many of the changes observed in the solubility of these gases

might occur over different seasons, particularly with N_2 and O_2. These *normal atmospheric equilibrium concentrations* (NAECs) are based on expected equilibrium conditions, between water and atmosphere, at a particular pressure, temperature, salinity, and humidity. However, there are many physical and biological factors that cause many gases to behave in a nonconservative manner resulting in deviations from predicted NAEC. For example, phytoplankton can rapidly alter O_2 concentrations via photosynthetic production of O_2. Similarly, bacteria can alter N_2 concentrations through denitrification and N_2 fixation processes, as well as CO_2 production from decomposition. Gas concentrations can also be altered by nonbiological processes such as Rn production via radioactive decay.

In situations where equilibrium conditions are not applicable, rates of gas exchange across the atmosphere–water boundary can be calculated using kinetic models (Broecker and Peng, 1974; Kester, 1975). The most common kinetic model used is the *stagnant film model* (Fig. 3.5). This model essentially has the following three regions of importance: (i) a well-mixed *turbulent atmospheric zone*, (ii) a *well-mixed thin-film* liquid zone, and (iii) a *laminar zone* separating the two turbulent regions. In the model, the thin film is considered permanent with a thickness defined as *z*. The average thickness of this film for the ocean has been estimated to be 17 µm (Murray, 2000), using isotope measurements (Broecker and Peng, 1974; Peng et al., 1979). There are uniform partial pressures of all gases in the turbulent zones, while liquid motion in the laminar zone flows parallel to the atmosphere–water interface. Movement of gases through the laminar zone is assumed to occur by molecular diffusion processes—this is the rate limiting step. It should also be noted that the stagnant film model is only for soluble and slightly soluble gases. For nonsoluble gases, the exchange of gases between the atmosphere–water interface is governed by their transport through the atmospheric boundary—making the dynamics very different.

By combining Henry's law (described earlier) with *Fick's first law* described by the following equation:

$$\frac{dC_i}{dt} = D_i \left[\frac{dC_i}{dz} \right] \qquad (3.11)$$

where C_i is the concentration of species I, t, the time, D_i, the diffusion coefficient, and dC_i/dz, the concentration gradient between the top and bottom of the thin film as represented by a vertical depth of z. The following equation can be used to describe the rate of gas flux through the atmosphere–water interface

TABLE 3.2 Solubilities of nitrogen, oxygen, argon, neon, and helium in seawater at a salinity of 35

t (°C)	N_2 (μmol/kg)	O_2 (μmol/kg)	Ar (μmol/kg)	Ne (nmol/kg)	He (nmol/kg)
0	616.4	349.5	16.98	7.88	1.77
5	549.6	308.1	15.01	7.55	1.73
10	495.6	274.8	13.42	7.26	1.70
15	451.3	247.7	12.11	7.00	1.68
20	414.4	225.2	11.03	6.77	1.66
25	382.4	206.3	10.11	6.56	1.65
30	356.8	190.3	9.33	6.36	1.64

Source: From Kester (1975).
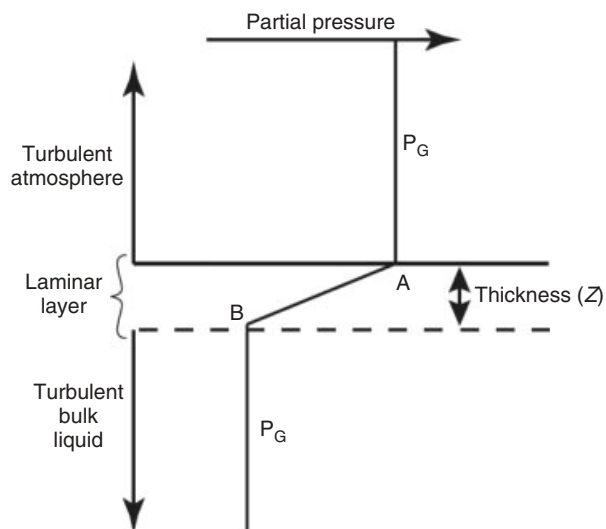
FIGURE 3.5 The most common kinetic model used to estimate rates of gas exchange across the atmosphere–water boundary is the stagnant film model. This model essentially has the following three regions of importance: (i) a well-mixed turbulent atmospheric zone (P_G), (ii) a well-mixed thin-film liquid zone (P_G), and (iii) a laminar zone (a and b) separating the two turbulent regions. The thin film is considered permanent with a thickness defined as z. *Source:* From Broecker and Peng (1974).

during disequilibrium:

$$\frac{dC_i}{dt} = \left(\frac{AD_i}{zK_H}\right)[P_i(\text{gas}) - P_A(\text{soln})] \qquad (3.12)$$

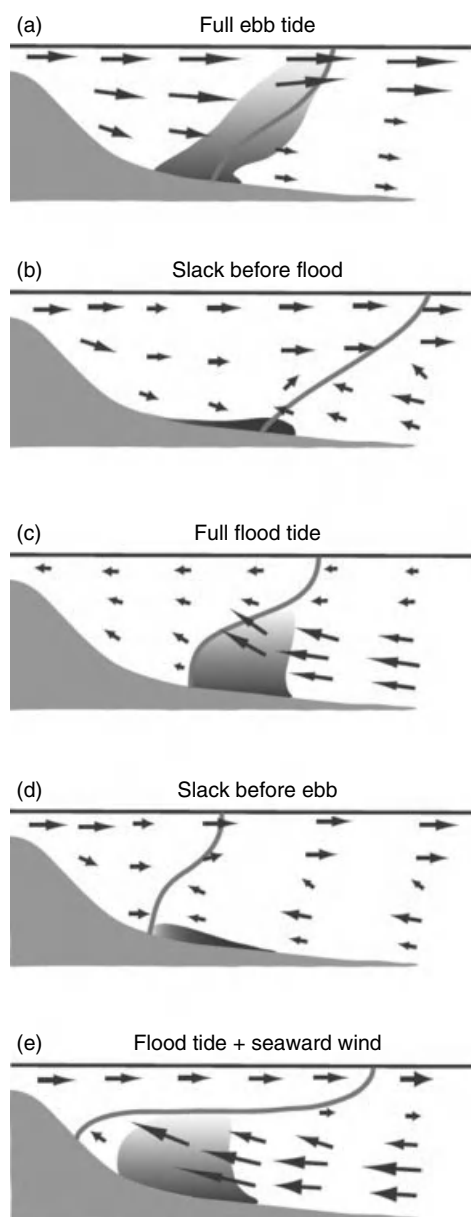where A is the interfacial area and K_H, Henry's law constant.

Implicit in this model is the assumption that molecular diffusivity and Henry's law constant are directly and inversely proportional, respectively, to the gas flux across the atmosphere–water interface. Molecular diffusion coefficients typically range from 1×10^{-5} to 4×10^{-5} cm^2/s and typically increase with temperature and decreasing molecular weight. Other factors such as thickness of the thin layer and wind also have important effects on gas flux. For example,

wind creates shear that results in a decrease in the thickness of the thin layer. The sea *surface microlayer* consists of films $50-100$ μm in thickness (Libes, 1992).

3.3 INTERFACES BETWEEN WATER AND SEDIMENT GEOCHEMISTRY

3.3.1 Estuarine Turbidity Maximum, Benthic Boundary Layer, and Fluid Muds

The *estuarine turbidity maximum* (ETM) is defined as a region where the suspended particulate matter (SPM) concentrations are considerably higher ($10-100$ times) than adjacent river or coastal end-members in estuaries (Schubel, 1968; Dyer, 1986). Some of the most extensive early work on the ETM, conducted in Chesapeake Bay, suggested that the primary mechanisms of particle trapping in ETMs were due to simple convergence at the limit of salt intrusion, in addition to slow particle settling (Schubel, 1968; Schubel and Biggs, 1969; Schubel and Kana, 1972; Nichols, 1974). A conceptual diagram illustrates that while the ETM roughly tracks the limit of salt, it is often decoupled from the salt front (defined here as the isohaline with a salinity of 1) due to a lag between ETM sediment resuspension/transport and rapid meteorologically driven movement of the salt front (Fig. 3.6; Sanford et al., 2001). Recent studies focused on sediment transport dynamics in the ETM have typically used acoustic Doppler profiles of velocity, acoustic backscatter, and optical backscatterrance sensors (Fain et al., 2001), in addition to remote sensing tools such as the sea-viewing wide field-of-view sensor (Uncles et al., 2001). Owing to rapid and high sedimentation rates in the ETM, the accumulation of particles in the *benthic boundary layer* (BBL) can result in the formation of *mobile* and *fluid muds*. The BBL is defined by Boudreau and Jorgensen (2001) as ''those portions of sediment and water columns that are

(a) Full ebb tide

(b) Slack before flood

(c) Full flood tide

(d) Slack before ebb

(e) Flood tide + seaward wind

FIGURE 3.6 A conceptual diagram showing that while the ETM roughly tracks the limit of salt, it was often decoupled from the salt front (defined here at the isohaline with a salinity of 1), due to a lag of ETM sediment resuspension/transport from rapid meteorologically driven movement of the salt front. *Source:* From Sanford et al. (2001) with permission.

affected directly in the distribution of their properties and processes by the presence of the sediment–water interface."

3.3.2 Early Diagenesis

Most modern estuarine systems have been filling with sediments since their formation about 5000–6000

years B.P. (Bianchi, 2007); this invokes long-term accumulation and storage of organic matter in these systems. The fate of SOM depends on the amount of early diagenesis that occurs in the upper sediments, which is largely controlled by the "quality" of organic detrital inputs (discussed above) and redox conditions of the sedimentary environment. Leeder (1982) defined *diagenesis* as "the many chemical and physical processes which act on sediment grains in the subsurface," which is further distinguished from *halmyrolysis*, defined as "a more restricted aspect of chemical changes operative at the sediment–water interface." Berner (1980) defined early diagenesis "as the changes occurring during burial to a few hundred meters where elevated temperatures are not encountered and uplift above sea level does not occur." This is the stage where key microbial and chemical transformations occur at low temperatures in recently deposited sediments, which has major effects on biogeochemical cycling in near-shore and estuarine environments.

Early diagenesis is typically described as a *steady-state phenomenon*; however, unless very long-term geological timescales are considered, steady-state conditions are generally not common in shallow turbid environments such as estuaries. There are many factors that contribute to these non-steady-state conditions, such as variations in sedimentation rate, inputs of organic matter, chemistry of bottom waters and sediments, bioturbation rates, and resuspension (Lasagna and Holland, 1976). Consequently, numerous attempts have been made to examine *non-steady-state diagenesis* over shorter time periods in estuarine systems (Mortimer et al., 1998; Deflandre et al., 2002).

As a result of particle settlement to the sediment-water interface, there is a mass accumulation of sediments, which results in compaction of sediments and the physical upward transport or *advection* of solutes in porewaters to the overlying water. Similarly, solutes in porewaters can also move by *diffusion* as a result of concentration gradients. Thus, porewaters can be transported by advection from burials, molecular diffusion, and biological pumping or irrigation (Aller, 2001; Jørgensen and Boudreau, 2001). Diffusion in aqueous environments occurs according to *Fick's laws of diffusion* (Berner, 1980).

Fick's first law, used for steady- and non-steady-state conditions, is as follows:

$$J_i = -D_i \left(\frac{\delta C_i}{\delta x} \right) \tag{3.13}$$

where J_i is the diffusional flux of component i in mass per unit area per time; D_i, the diffusion coefficient of i in area per unit time; C_i, the concentration of

component i in mass per unit time; x, the direction of maximum concentration gradient; and the negative sign, the flux in the opposite direction of the gradient. *Fick's second law*, used for steady- and non-steady-state conditions, is as follows:

$$\frac{\delta c_i}{\delta t} = \frac{D_i(\delta^2 c_i)}{\delta x} \qquad (3.14)$$

To apply Fick's laws to solute fluxes in sediments, adjustments have to be made to these equations to account for the negative interference effects that sediment particles have on the diffusion of solutes in pore waters (Lerman, 1979; Berner, 1980).

After making these adjustments for diffusion in sediments, the mass balance and vertical concentration patterns of nonconservative solutes in saturated sediments can be described by the following one-dimensional *advective–diffusive* general diagenetic equation (GDE; Berner, 1980; Aller, 2001; Jørgensen and Boudreau, 2001):

$$\frac{\delta \varphi C}{\delta t} = \varphi D_s \left(\frac{\delta^2 c}{\delta x^2} \right) - \frac{\delta \omega_p C}{\delta x} - \sum R_i \qquad (3.15)$$

where C is the concentration of solute, t, the time, D_s, the whole sediment diffusion coefficient of solute C, x, the sediment depth relative to surface ($x = 0$), ω_p, the pore water advection velocity relative to the sediment–water interface, and ΣR_i, the sum of all reactions affecting solute C. These types of diagenetic models have been commonly used to describe the distribution of redox-sensitive metals (e.g., Mn and Fe) because of their close association with the mineralization of organic matter in sediments (Burdige, 1993; Jørgensen and Boudreau, 2001). In particular, a number of steady-state models have been used to describe the diagenesis of Mn and Fe (more details on this later in chapter) in sediments (Aller, 1990; Boudreau, 1996; Overnell, 2002). In a recent study on sediments in the Loch Etive estuary (Scotland), diagenetic processes based on reactive Mn and Fe oxides as electron acceptors were compared using the diagenetic models of van Cappellen and Wang (1996) and Slomp et al. (1997). It was concluded that there was both considerable agreement and disagreement in the modeled sediment profiles of Mn and Fe and that the application of multiple diagenetic models is strongly encouraged for comparison (Overnall, 2002). When examining biological mixing as a one-dimensional diffusive process, bioturbation and biodiffusion coefficients are used in the GDE similar to standard Fickian diffusivity (Wheatcroft et al., 1991). The justification for using a biodiffusion coefficient (D_B) is because it is assumed that all biological mixing activities are integrated over time—thereby making it a diffusion-like

process. Estimates of D_B can be made using a regression of down-core distribution of radionuclides.

3.4 BIOGEOCHEMISTRY OF ORGANIC MATTER

3.4.1 Particulate and Dissolved Organic Matter in Estuaries

The photosynthetic fixation of inorganic carbon and nutrients into plant biomass is the primary source of organic matter within estuaries (Bauer and Bianchi, ; Bianchi and Bauer,). Therefore, it is critical to have some basic understanding about the primary producer community in estuaries (e.g., phytoplankton, benthic macroalgae, microphytobenthos, seagrasses, and wetland plants), in addition to the habitats and conditional constraints needed for growth (Chapters 5–8). Inputs of dissolved organic matter (DOM), particulate organic matter (POM), and nutrients to estuaries can occur from both coastal ocean and riverine end-members, which support both autotrophic and heterotrophic production in different estuarine regions.

Estuarine DOM comprises a diverse array of allochthonous and autochthonous sources (see reviews by Cauwet, 2002; Findlay and Sinasbaugh, 2003; Bauer and Bianchi,). These major sources primarily comprise riverine inputs, autochthonous production from algal and vascular plant sources, benthic fluxes, groundwater inputs, and exchange with adjacent coastal systems (Fig. 3.7). In coastal and open ocean waters, DOM is generally positively correlated with phytoplankton biomass (Hansell and Carlson, 2002; Santschi et al., 1995). It has been estimated that phytoplanktons release approximately 12% of total primary production as dissolved organics over a range of freshwater to marine environments (Baines and Pace, 1991). However, water column DOM in many estuarine systems does not show positive correlations with phytoplankton biomass because of allochthonous inputs from soils and vascular plants that are hydrologically coupled to these wetland systems (Argyrou et al., 1997; Harvey and Mannino, 2001; Jaffe et al., 2004).

Past work has shown that DOM from river/estuarine systems is primarily derived from terrestrial vegetation and soils (Malcolm, 1990; Opsahl and Benner, 1997). In fact, some of the highest DOM estuaries in the US border the Gulf of Mexico (Guo et al., 1999; Engelhaupt and Bianchi, 2001), a region that also has some of the highest rates of fresh litter decomposition in soils (Meentemeyer, 1978).
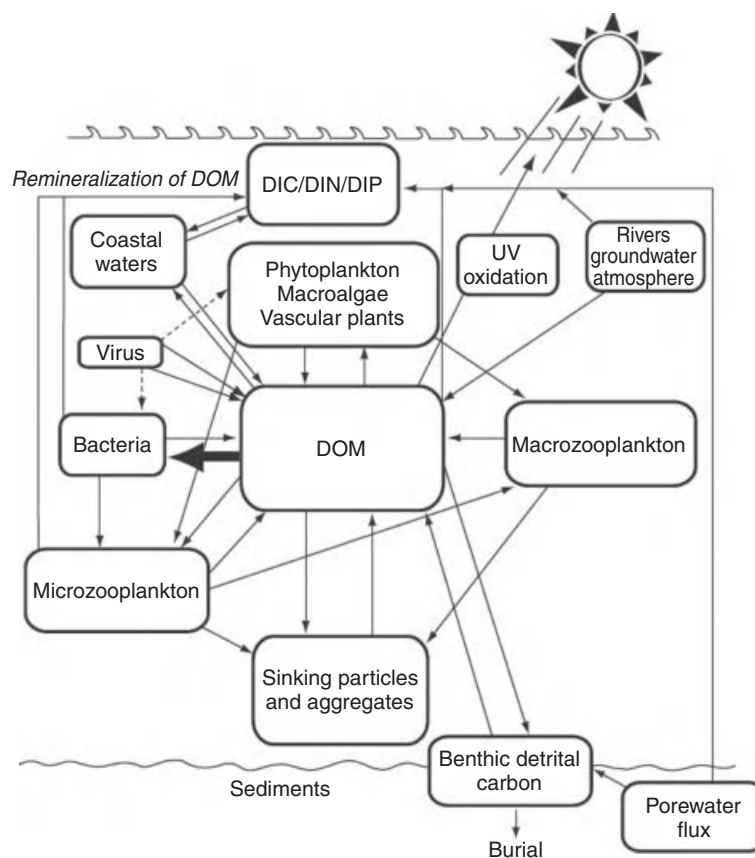
FIGURE 3.7 Major sources of dissolved organic matter (DOM) to estuaries, primarily comprise riverine inputs, autochthonous production from algal and vascular plant sources, benthic fluxes, groundwater inputs, and exchange with adjacent coastal systems. *Source:* Modified from Hansell and Carlson (2002).

Riverine/estuarine DOM is generally considered to be recalcitrant and transported conservatively to the ocean (Moore et al., 1979; van Heemst et al., 2000). However, spatial variability in the abundance of phytoplankton exudates (Aminot et al., 1990; Fukushima et al., 2001), uptake of DOM by bacteria (Zweifel, 1999; Pakulski et al., 2000), chemical removal processes (e.g., *flocculation, deflocculation, adsorption, aggregation*, and *precipitation*; Sholkovitz, 1976; Sholkovitz et al., 1978; Lisitzin, 1995), inputs from porewaters during resuspension events (Burdige and Homstead, 1994; Middelburg et al., 1997), and atmospheric inputs (Velinsky et al., 1986) can all contribute to nonconservative behavior in estuaries.

It is well known that DOM exists in different size fractions in aquatic systems (Sharp, 1973) and that a large portion estuarine DOM is composed of colloidal organic matter (Filella and Buffle, 1993; Guo and Santschi, 1997; Cauwet, 2002; Bianchi, 2007). The characterization of different size classes of DOM is established by physical separation through filters/membranes of differing pore sizes; thus, colloids are an operationally defined fraction of the total DOM in the size range of $0.001-1\,\mu m$ (Vold and Vold, 1983). Unfortunately, using size as the primary criteria for characterizing colloids can be very misleading when considering the biochemical differences associated with these different size fractions and their reactivity with contaminants (Gustafsson and Gschwend, 1997; Benner, 2002).

Another term commonly used in association with DOM is *humic substances*; humic substances are typically defined as complex assemblages of molecules that have a yellow-to-brown color and are derived from plants and soils (Hatcher et al., 2001). Humic substances represent a large fraction of what is termed *chromophoric dissolved organic matter* (CDOM) in aquatic systems around the world (Blough and Green, 1995). Aquatic humic substances can further be categorized as *fulvic acids, humic acids*, and *humin* based on the solubility in acid and base solutions (Schnitzer and Khan, 1972; McKnight and Aiken, 1998). More specifically, humic acids typically have a molecular weight of greater than 100,000 Da

and are soluble above a pH of 2: fulvic acids that are smaller molecules (~500 Da) are soluble at any pH, and humin is not soluble across a full pH range (McKnight and Aiken, 1998).

Sediments may also represent an important source of DOM to the water column of shallow estuarine systems (Burdige, 2006, Bianchi, 2007). The accumulation of DOM in porewaters results from the diagenesis of sedimentary organic carbon into a complex mixture of macromolecules (e.g., humic substances) and smaller monomeric forms (e.g., amino acids; Orem et al., 1986; Burdige, 2002, 2006). The flux of porewater DOM across the sediment–water interface represents an important source to the total DOM pool in estuaries (Alperin et al., 1992; Argyrou et al., 1997; Middelburg et al., 1997; Burdige, 2001, 2002). It has been suggested that benthic fluxes are a significant source to coastal and estuarine systems (0.9×10^{14} g C/year) and may represent about the same magnitude as riverine inputs of DOC to the ocean ($2-2.3 \times 10^{14}$ C/year; Burdige et al., 1992; Burdige and Homstead, 1994). The role of porewater DOM that gets entrained in the *benthic nepheoloid layer*, from resuspension events of estuarine and shelf sediments, may also be important in affecting the composition and age of DOM in shelf and deeper slope waters (Guo and Santschi, 2000; Mitra et al., 2000). Similarly, porewaters contribute to the protein or amino acid-like fluorescence signature of the water column; maximum concentrations of these signals have been observed at the sediment–water interface (Coble, 1996).

3.4.2 Decomposition of Organic Detritus

Organic detritus has long been recognized for its importance as a food resource and its influence on overall biogeochemical cycling in coastal systems (Tenore et al., 1982; Rice, 1982; Mann and Lazier, 1991). Major contributors of organic detritus in estuarine systems are decaying plant materials and animal fecal pellets. Vascular plant detritus is particularly important in many estuarine systems (Chapters 5–7); this refractory material typically requires the activity of microbial communities to convert lignocellulosic polymers into more labile available food resources for higher consumers (Moran and Hodson, 1989a,b). The decay of aquatic organic detritus is generally divided into (i) *leaching*, (ii) *decomposition*, and (iii) *refractory* phases (Odum et al., 1973; Rice and Tenore, 1981; Webster and Benfield, 1986).

In the *leaching phase*, soluble compounds are rapidly lost from fresh detritus over a scale of minutes to weeks (Fig. 3.8; Wilson et al., 1986). In the case of the marsh plant *Spartina alterniflora*, as much as 20–60% of the original material can be lost during this phase
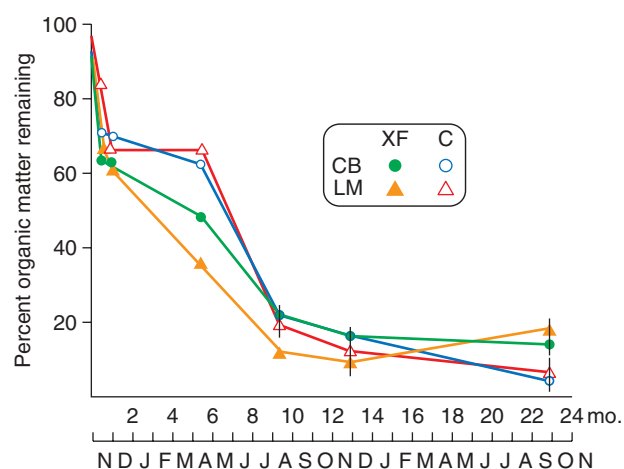
FIGURE 3.8 Percent organic matter remaining during a 23-month decay experiment with *S. alterniflora* detritus. *Source:* Modified from Wilson et al. (1986).

(Wilson et al., 1986). These soluble DOM compounds released from detrital particles are rapidly used by bacteria in the surrounding water column (Aneiso et al., 2003). Much of this leached material likely comprise short-chain carbohydrates, proteins, and fatty acids (Dunstan et al., 1992; Harvey et al., 1995). There has also been considerable debate about the rate of decay of these labile leached substrates in oxic versus anoxic conditions, with some studies showing faster decay under oxic conditions (Bianchi et al., 1991; Sun et al., 1993; Harvey et al., 1995) and others showing no effects of redox (Henrichs and Reeburgh, 1987; Andersen, 1996).

The *decomposition phase* involves the heterotrophic breakdown of detritus by microbes and metazoans (e.g., *detritivores* and *deposit-feeders*). Nitrogenous compounds of micro- and macroalgae are more likely to contribute to the nutrition of detritivores than those of vascular plants (Findlay and Tenore, 1982). As microorganisms colonize detritus during this phase, there is a relative increase in the nitrogen content of the ''aging'' detritus (Darnell, 1967; Tenore et al., 1982; Rice and Hanson, 1984). Earlier studies proposed that most of the nitrogen could be equated with ''protein enrichment'' from microbes (Newell, 1965; Odum et al., 1973). However, further work showed that the presence of nonprotein nitrogen in plant detritus (Suberkropp et al., 1976) and enrichment from complexation (physical and chemical) in *humic geopolymers* (Hobbie and Lee, 1980; Rice, 1982; Rice and Hanson, 1984) suggested that protein-N was not the only source. Adsorption of NH_4^+ by detritus may have also added to the total N (Mackin and Aller, 1984). The attached bacteria are considered to

be more active than the surrounding free bacteria (Griffith et al., 1994) and are critical in the breakdown of refractory compounds.

Vascular plants contain more ligneous and phenolic compounds, which can also reduce resource availability to consumers (Valiela et al., 1979; Rice and Tenore, 1981; Bianchi, 2007). *Secondary plant compounds* such as phenols, alkaloids, tannins, organic acids, saponins, terpenes, steroids, essential oils, and glycosides can deter herbivory and detritivory (Rietsma et al., 1982). For example, tannins are phenolic compounds known to inhibit microbial activity through the precipitation of enzyme proteins (Janzen, 1974). Similarly, C_4 plants (e.g., *S. alterniflora, Spartina patens*, and *Distichlis spicata*) produce cinnamic acids (e.g., ferulic and *p*-coumaric acids), which inhibit herbivory more effectively than comparable C_3 marsh plants (*Juncus* spp.; Haines and Montague, 1979; Valiela, 1995). The presence of these secondary compounds generally results in slower decay rates for vascular versus nonvascular plants (Valiela 1995). The final *refractory phase* is characterized by detritus composed of lignin and cellulose, which decay very slowly (Maccubbin and Hodson, 1980; Wilson et al., 1986). The source of detritus will clearly affect the time period of refractory decay.

Berner (1980) first introduced the following concept of a ''one-G'' model for determining first-order decay constants (k) of organic matter decomposition:

$$G_t = G_0 e^{-kt} \qquad (3.16)$$

where G_t is the mass of detritus at time t and G_0, the initial mass of detritus. Although this model appeared to work well in calculating decay constants for predominantly labile sources of organic matter such as macro- and microalgae, there were problems with more refractory sources of detritus such as *Spartina* (Rice and Hanson, 1984). To better describe the decay dynamics of refractory detritus, which generally contain both labile and refractory biochemical components, the following ''two-G'' model was developed by Rice and Hanson (1984):

$$G_t = G^* + G_{10} e^{-k_1 t} \qquad (3.17)$$

where G^* is the constant mass of refractory material, defined by $G^* = G - G_1, G$ is the total mass of the detritus and G_1 is the labile material, G_{10} is the initial mass of labile material, and k_1 is the decay constant of labile material.

In a decomposition experiment comparing decay dynamics of macroalgal (e.g., *Gracilaria foliifera*) and vascular plant (e.g., *S. alterniflora*) detritus, it was found that the two-G model proved more precise in calculating decay constants over shorter time intervals (days) compared with the one-G model, which works relatively well over weeks to months (Rice and Hanson, 1984). Similarly, Westrich and Berner (1984) performed laboratory experiments to show that decomposition of phytodetritus in sediments can be separated into two decomposable fractions—with significant differences in reactivity and a highly refractory (nonmetabolozable) fraction. This work established, for the first time, that organic matter decomposition in sediments can be described by a multi-G model.

3.4.3 Characterization of Organic Matter Using Biomarker Techniques

In general, estuarine organic matter is derived from a multitude of natural and anthropogenic allochthonous and autochthonous sources that originate across a freshwater to seawater continuum. Knowledge of sources, reactivity, and fate of organic matter are critical in understanding the role of estuarine and coastal systems in global biogeochemical cycles (Hedges and Keil, 1995; Bianchi and Canuel, 2001, 2011). Owing to a wide diversity of organic matter sources and the dynamic mixing that occurs in estuarine systems, it remains a significant challenge to determine the relative importance of these source inputs to biogeochemical cycling in the water column of sediments. Temporal and spatial variability in organic matter inputs adds further to the complexity in understanding these environments. In recent years, there have been significant improvements in our ability to distinguish between organic matter sources in estuaries using tools such as elemental, isotopic (bulk and compound/class specific), and chemical biomarker methods.

3.4.3.1 Bulk Organic Matter Techniques

The abundance and ratios of important elements in biological cycles (e.g., C, H, N, O, S, and P) provide the basic foundation of information on organic matter cycling. For example, concentrations of total organic carbon (TOC) provide the most important indicator of organic matter since approximately 50% of most organic matter comprises C. TOC in estuaries is derived from a broad spectrum of sources with very different structural properties and decay rates (Bianchi, 2007; Bianchi and Bauer, ; Bianchi and Canuel, 2011). Consequently, while TOC measurements can provide essential information on spatial and temporal dynamics of organic matter, it lacks any specificity to source or age of the material.

When bulk C information is combined with additional elemental information, as in the case of the

C to N (C:N) ratio, basic source information can be inferred about algal and terrestrial source materials (see review by Meyers, 1997). The broad range of C:N ratios across divergent sources of organic matter in the biosphere demonstrate how such a ratio can provide an initial proxy for determining source information (Table 3.3). The basic reason for such differences in C:N ratios between vascular plants (>17) and microalgae (5–7) is simply due to the carbohydrate-rich (e.g., cellulose)/protein-poor and protein-rich/carbohydrate-poor nature of each source, respectively. The most abundant carbohydrates supporting this high C content in vascular plants are structural polysaccharides such as cellulose, hemicellulose, and pectin (Aspinall, 1970). Recent work estimated the relative importance of terrestrial versus marine sources in coastal sediments, using a simple mixing model based on C:N weight ratios of 6 for the marine (Muller, 1977) and 13 for the terrestrial (Parrish et al., 1992) end-members of organic matter (Colombo et al., 1996a, 1996b). However, C:N ratios can be very misleading in determining organic matter sources in the absence of additional source proxies. In some cases, selective utilization of N, due to N limitation in a system, can result in artificially high C:N ratios and misidentification of source materials. Finally, artifacts from the standard procedure of removing carbonate carbon when measuring TOC can also alter C:N ratios (Meyers, 2003). Specifically, after removing carbonate, a residual N made up of both inorganic and organic N remains—which is why the N used in C:N ratios is defined as total nitrogen. In most cases, the inorganic component of this residual N is relatively small in sedimentary and water column sources of organic matter. However, in sediments having very low concentrations of organic matter (e.g., <0.3%), the relative importance of this residual inorganic N could be significant, resulting in underestimates of C:N ratios (Meyers, 2003). More specifically, this results from NH_4^+ adsorption on low organic content sediments. Fortunately, most estuarine sediments are greater than 1% organic matter generally making this artifact relatively minor.

3.4.3.2 Isotopic Mixing Models

End-member mixing models have been used to evaluate sources of dissolved inorganic nutrients (C, N, and S; Day et al., 1989; Fry, 2002) and organic matter (POM and DOM; Raymond and Bauer, 2001a,b; Gordon and Goni, 2003; McCallister et al., 2004; Bauer and Bianchi, ; Bianchi and Bauer,) in estuaries. However, due to significant overlap in stable isotopic signatures, it has proven difficult to discern multiple sources of
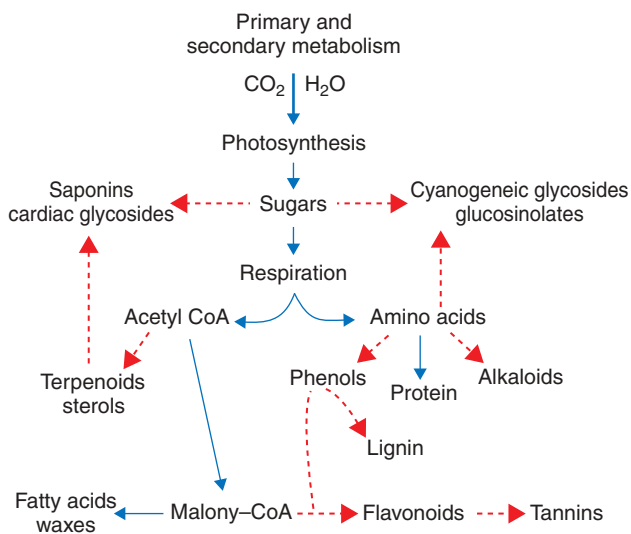
TABLE 3.3 Approximate carbon to nitrogen ratios in some terrestrial and marine producers[a]

		C/N
Terrestrial	Leaves	35–100
	Wood	1000
Marine vascular plants	Zostera marina	17–70
	Spartina alterniflora	24–45
	Spartina patens	37–41
Marine macroalgae	Browns (Fucus, Laminaria)	30 (16–68)
	Greens	10–60
	Reds	20
Microalgae and microbes	Diatoms	6.5
	Greens	6
	Blue-greens	6.3
	Peridineans	11
	Bacteria	5.7
	Fungi	10

[a]Data compiled in Fenchel and Jorgensen (1977), Alexander (1977), Fenchel and Blackburn (1979), and data of I. Valiela and J. M. Teal.
Source: Modified from Valiela (1995).

dissolved and particulate constituents, when using single and dual bulk isotopes in complex systems (Cloern et al., 2002). More recently, new approaches using end-member mixing models that utilize multiple isotopic tracers coupled with chemical biomarker measurements have proven useful. The application of stable isotopes as tracers of organic matter sources in aquatic systems has been quite extensive (Lajtha and Michener, 1994; Michener and Schell, 1994). Many studies have also used end-member values from a combination of stable and radiocarbon isotopes and biomarkers (e.g., lignin phenols and lipids) to determine carbon sources in coastal systems (e.g., Goñi et al., 1998; Raymond and Bauer, 2001a,b; McCallister et al., 2004). The range of isotopic $\delta^{13}C$ and $\delta^{15}N$, respectively, values for organic matter sources in a number of estuaries are as follows: terrigenous (vascular plant), −26 to −30 and −2 to +2 (Fry and Sherr, 1984; Deegan and Garritt, 1997); terrigenous soils (surface)/forest litter, −23 to −27 and 2.6 to 6.4 (Cloern et al., 2002; Richter et al., 1999); freshwater phytoplankton, −24 to −30 and 5 to 8 (Sigleo and Macko, 1985); marine/estuarine phytoplankton, −18 to −24 and 6 to 9 (Fry and Sherr, 1984; Currin et al., 1995); C-4 salt marsh plants, −12 to −14 and 3 to 7 (Fry and Sherr, 1984; Currin et al., 1995); benthic microalgae, −12 to −18 and 0 to 5 (Currin et al., 1995); C-3 freshwater/brackish marsh plants, −23 to −26 and 3.5 to 5.5 (Fry and Sherr, 1984). Many of

Primary and
secondary metabolism

CO_2 | H_2O

Photosynthesis

Saponins
cardiac glycosides ◄----- Sugars -----► Cyanogeneic glycosides
glucosinolates

Respiration

Acetyl CoA ◄   ► Amino acids

Terpenoids
sterols   Phenols   Alkaloids
                 Protein

Lignin

Fatty acids
waxes ◄ Malony–CoA ----► Flavonoids ---► Tannins

FIGURE 3.9 Pathways of the sum of all biochemical processes is called *metabolism*. It is differentiated as primary and secondary metabolism. Primary metabolism contains all pathways necessary to keep the cell alive, whereas in secondary metabolism, compounds are produced and broken down that are essential for the entire organism.

the early investigations were based on a two end-member mixing model (binary) in which the more depleted terrestrial $\delta^{13}C$ end-member could be used along with the more enriched marine phytoplankton end-member to establish their relative abundance throughout the estuary. For example, the following binary equation could be used to determine percent terrestrial organic matter in an estuary:

$$\% \, OC_{Terr} = \frac{(\delta^{13}C_{sample} - \delta^{13}C_{marine})}{(\delta^{13}C_{riverine} - \delta^{13}C_{marine})} \qquad (3.18)$$

where $\delta^{13}C_{sample}$ is the isotopic composition of a sample, $\delta^{13}C_{marine}$, the published isotopic value of marine phytoplankton (using the end-member listed above values), and $\delta^{13}C_{riverine}$, the published isotopic values of riverine POM (using the end-member values listed above).

Recent work compared the effectiveness of binary and three end-member models in determining the relative abundance of marine versus terrestrial sources off the Atchafalaya and Mississippi River estuaries (Gordon and Goñi, 2003; Bianchi et al., 2011). The authors suggested that it was important to use a three end-member model that combines both biomarkers and stable isotopes for three organic carbon source end-members (soils and/or marsh, riverine, and marine). This separates the terrestrial end-member into two different sources, vascular plants and soils.

3.4.3.3 Molecular Biomarkers

Owing to the complexity of organic matter sources in estuaries and the aforementioned problems associated with making only bulk measurements to constrain them, the application of chemical biomarkers has become widespread in estuarine research (Bianchi and Canuel, 2001; Bianchi, 2007; Bianchi and Canuel, 2011, and references therein). The term *biomarker molecule* was recently defined by Meyers (2003) as ''compounds that characterize certain biotic sources and that retain their source information after burial in sediments, even after some alteration.'' This molecular information is more specific and sensitive than bulk elemental and isotopic techniques in characterizing sources of organic matter and further allows for identification of multiple sources (Meyers, 1997, 2003).

The *catabolic* and *anabolic* pathways that are responsible for the formation of many of the biomarker compounds discussed in this chapter occur through an ''intermediary'' metabolism via *glycolysis* and the *citric acid cycle* (Voet and Voet, 2004). The biosynthetic pathways of these compounds can be divided into primary and secondary metabolism (Fig. 3.9). Many of these compounds are not used as chemical biomarkers in estuarine research but are shown here to simply illustrate their relationship with the biomarkers discussed in this chapter. For more details on the biosynthetic pathways illustrated here and applications in estuaries, please refer to the study by Voet and Voet (2004) and Bianchi (2007), respectively.

3.5 MACRONUTRIENT CYCLING

3.5.1 Sources of Nitrogen in Estuaries

Elemental nitrogen (N_2) makes up 80% of the atmosphere (by volume) and represents the dominant form of atmospheric nitrogen gas. Despite its high atmospheric abundance, N_2 is generally nonreactive, owing to strong triple bonding between the N atoms, making much of this N_2 pool unavailable to organisms. In fact, only 2% of this N_2 pool is believed to be available to organisms at any given time (Galloway, 1998). Consequently, N_2 must be ''fixed'' into ionic forms such as NH_4^+ before it can be used by plants. Since N is essential for the synthesis of amino acids and proteins and because it is often in low concentrations, N is usually considered to be limiting to organisms in many ecosystems. Nitrogen has five valence electrons and can occur in a broad range of oxidation states that range from +V to −III,

with NO_3^- and NH_4^+ being the most oxidized and reduced forms, respectively. Some of the most common N compounds that exist in nature, along with their boiling points, ΔH^0, and ΔG^0, are shown in Table 3.4 (Jaffe, 2000); these thermodynamic data can be used to calculate equilibrium concentrations.

Nitrogen cycling in estuaries is in general affected by inputs of N from surface and groundwaters, atmospheric wet and dry fallout, as well as N recycling in both the water column and sediments (Fig. 3.10; Paerl et al., 2002). Dominant inputs of N to estuaries are linked with freshwater inputs from rivers (Nixon et al., 1995, 1996; Boynton and Kemp, 2000; Seitzinger et al., 2002a; Bouwman et al., 2005). Many of these nitrogen inputs have increased in rivers and estuaries around the world as a direct result of human expansion (Peierls et al., 1991; Howarth et al., 1996; Bouwman et al., 2005). Current inputs of N to Atlantic and Gulf coast US estuaries are 2–20 times higher than in the preindustrialized periods (Howarth et al., 1996, Goolsby, 2000).

Nitrogen inputs to watersheds, which result in DIN export to coastal systems, often lead to enhanced primary production, since many estuaries are N limited (Nixon, 1986, 1995; D'Elia et al., 1992; Howarth et al., 2000). This can result in the formation of harmful algal blooms as well as *hypoxia* and anoxic water columns (Boynton et al., 1995; Paerl, 1997; Richardson, 1997). Submarine groundwater discharge (SGD) of N to estuaries is also important, particularly, although not exclusively, in systems dominated by karst geomorphology, and where surface/river inputs are minimal. One such area is in northern Yucatan (Mexico), where concentrations of NO_3^- and NH_4^+ in SGD entering local lagoons, range from 20 to 160 μM and 0.1 to 4 μM, respectively (Herrera-Silveira, 1994). Seasonal pulsing of SGD, driven by precipitation events, has not resulted in any extensive eutrophication in these lagoons (Pennock et al., 1999).

Dissolved organic nitrogen (DON) can represent a significant fraction of the total dissolved nitrogen (TDN) in rivers and estuaries, respectively (Berman and Bronk, 2003). Sources of DON to estuaries may be derived from actively growing phytoplankton communities, where small molecules such as dissolved free amino acids (DFAAs) are released—which are highly available to bacteria, but represent only a small percent of the total DON (ca. <10%; Diaz and Raimbault, 2000; Bronk, 2002). DON typically represents about 60–69% of the TDN in rivers and estuaries (Berman and Bronk, 2003). The major components of DON include urea, dissolved combined amino acids, DFAA, proteins, nucleic acids, amino sugars, and humic substances (Berman and Bronk, 2003). However, less than 20% of DON is chemically characterized.

3.5.2 Transformations of Inorganic and Organic Nitrogen

The major processes involved in the biogeochemical cycling of N in estuaries and the coastal ocean are (i) biological N_2 fixation (BNF), (ii) ammonia assimilation, (iii) nitrification, (iv) assimilatory NO_3^- reduction, (v) ammonification or N-remineralization,

TABLE 3.4 Chemical data on important nitrogen compounds in the environment

| Oxidation State	Compound	b.p. (°C)	$\Delta H^0(f)$	$\Delta G^0(f)$ (kJ/mol, 298 K)
+5	$N_2O_5(g)$	11	115	+5
+5	$HNO_3(g)$	83	−135	−75
+5	$Ca(NO_3)_2(s)$		−900	−720
+5	$HNO_3(aq)$		−200	−108
+4	$NO_2(g)$	21	33	51
+4	N_2O_4		9	98
+3	$HNO_2(g)$		−80	−46
+3	$HNO_2(aq)$		−120	−55
+2	$NO(g)$	−152	90	87
+1	$N_2O(g)$	−89	82	104
0	$N_2(g)$	−196	0	0
−3	$NH_3(g)$	−33	−46	−16.5
−3	$NH_4(aq)$		−72	−79
−3	$NH_4Cl(s)$		−201	−203
−3	$CH_3NH_2(g)$		−28	28
−3	$H_2O(g)$	100	−242	−229

Source: Modified from Jaffe (2000).
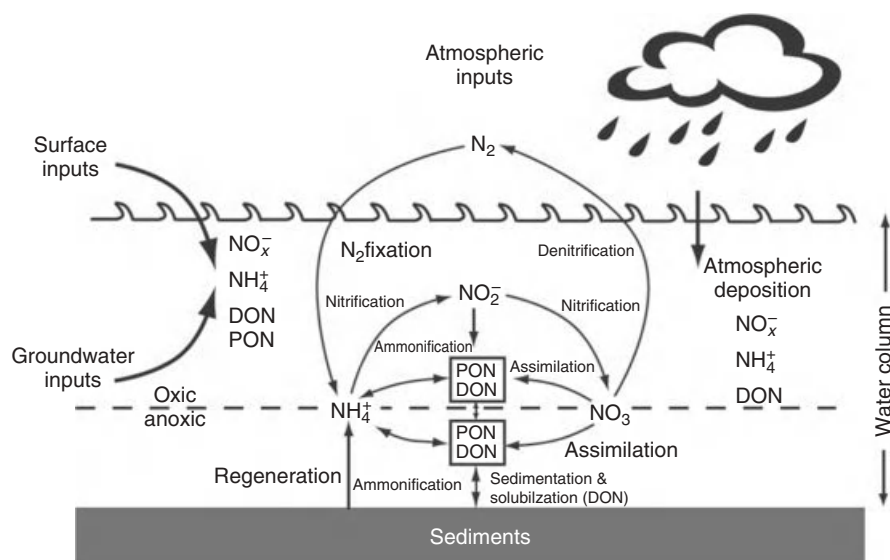
FIGURE 3.10 Schematic of nitrogen sources and cycling in estuaries. These sources include a diverse group of diffuse point and nonpoint agricultural, urban, and rural sources (e.g., wastewater, industrial discharges, stormwater, and overflow discharges) across a broad spectrum of watersheds (e.g., urban, agricultural, and upland and lowland forests. *Source:* Modified from Paerl et al. (2002).

(vi) ammonium oxidation, (vii) denitrification and dissimilatory NO_3^- reduction to NH_4^+, and (viii) assimilation of DON (Fig. 3.11; Libes, 1992). These processes are essentially driven by bacteria, as discussed in the following section, and are in some cases energy producing, or may occur in *symbiosis* with another organism. These heterotrophic processes can result in both additions (e.g., N_2 fixation) and losses of N (e.g., denitrification) within estuaries.

BNF is a process performed by prokaryotic (both heterotrophic and phototrophic) organisms (sometimes occurring symbiotically with other organisms) resulting in the enzyme-catalyzed reduction of N_2

to NH_3 or NH_4^+ or organic nitrogen compounds (Jaffe, 2000). Organisms that fix N_2 are also called *diazotrophs*. The high activation energy required to break the triple bond makes BNF an energetically expensive process for organisms—thereby restricting BNF to select groups of organisms. BNF is an important process in aquatic systems (Howarth et al., 1988a,b).
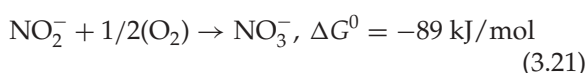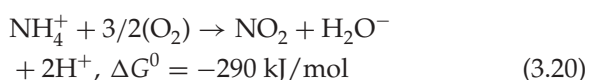
Ammonia assimilation is where NH_3 or NH_4^+ is taken up and incorporated into organisms as organic nitrogen molecules (Jaffe, 2000), as shown below for NH_4^+:

$$NH_4^+ \rightarrow N(NH_3)\text{-organic} \qquad (3.19)$$
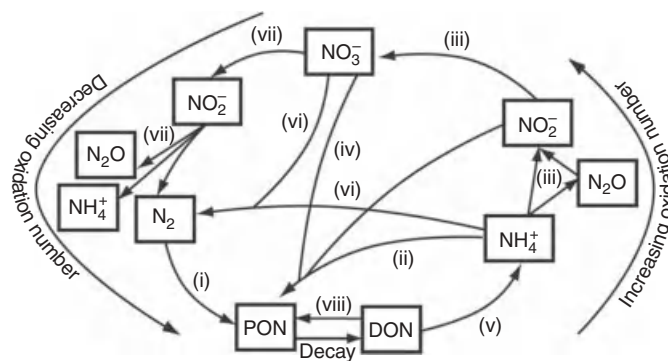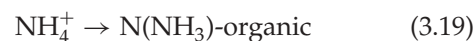
FIGURE 3.11 Major processes involved in the biogeochemical cycling of N in estuaries and the coastal ocean: (i) biological N_2-fixation (BNF), (ii) ammonia assimilation, (iii) nitrification, (iv) assimilatory NO_3^- reduction, (v) ammonification or N-remineralization, (vi) ammonium oxidation (speculative at this time), (vii) denitrification and dissimilatory NO_3^- reduction to NH_4^+, and (viii) assimilation of dissolved organic nitrogen (DON). *Source:* Modified from Libes (1992).

The ability to take up these reduced forms of N is a distinct energetic advantage for organisms because it is a direct means of getting a reduced form of N, unlike the uptake of NO_3^-, which requires the extra step of NO_3^- reduction. However, some phytoplankton prefer NO_3^- over NH_4^+ as an N source. In estuaries, NH_4^+ is generally the most dominant form of DIN in sediments; however, some pools of NH_4^+ are unavailable for uptake because they are bound within the internal matrix of minerals (Rosenfield, 1979; Krom and Berner, 1980).

Nitrification is where NH_3 or NH_4^+ is oxidized to NO_2^- or NO_3^- through the following two energy-producing reactions (Delwich, 1981):

$$NH_4^+ + 3/2(O_2) \rightarrow NO_2 + H_2O^-$$
$$+ 2H^+, \Delta G^0 = -290 \text{ kJ/mol} \quad (3.20)$$

$$NO_2^- + 1/2(O_2) \rightarrow NO_3^-, \Delta G^0 = -89 \text{ kJ/mol} \quad (3.21)$$

Equation 3.20 involves the oxidation of NH_4^+ to NO_2^- and is primarily performed by bacteria of the genus *Nitrosomonas* (some species of the genus *Nitrocystis* sp. are also capable; Day et al., 1989), and Equation 3.21 is the continued oxidation of NO_2^- to NO_3^-, performed by bacteria of the genus *Nitrobacter* spp. During this process of NH_4^+ oxidation, these bacteria use CO_2 as their source of C to be fixed into organic compounds. Hence, these bacteria are considered to be *chemoautotrophs* because they gain their energy by chemical oxidation and are autotrophs because they do not rely on external sources of organic matter. Finally, nitrification requires O_2, thus the activity of these nitrifying bacteria require in sediments is particularly sensitive to the absence of dissolved oxygen (Kemp et al., 1982, 1990).

Assimilatory NO_3^- reduction to NH_4^+ involves the simultaneous reduction of NO_3^- and uptake of N by the organism into biomass, as shown below:

$$NO_3^- + H^+ \rightarrow NH_3\text{-organic} \quad (3.22)$$
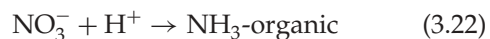
This pathway is particularly dominant when reduced forms of N are low, such as oxic water columns in estuaries. This represents an important pathway for the uptake of N by estuarine organisms capable of uptake of both reduced and oxidized forms of N.

Ammonification is the process where NH_3 or NH_4^+ is produced during the breakdown of organic nitrogen by organisms (also called *N-remineralization*). In the case of the most dominant nitrogen-containing organic compounds, proteins, peptide linkages are broken down followed by *deamination* of amino acids to produce NH_3 or NH_4^+. Ammonification is the conversion of DON to ammonium (DON $\rightarrow NH_4^+$).

This process occurs through the decay of plants and animals mediated by heterotrophic bacteria (Nowicki and Nixon, 1985) or through excretion from animals (Bianchi and Rice, 1988; Gardner et al., 1993).

Ammonium oxidation (*anammox*), which involves the anaerobic NH_4^+ oxidation with NO_3^-, may be another mechanism, whereby N is lost from estuarine/coastal systems. This process has been shown to represent from 20% to 67% of N_2 production in temperate continental shelf sediments (Thamdrup and Dalsgaard, 2002); however, only limited knowledge currently exists on the pathways of anammox in natural systems. It does appear that the optimal conditions for anammox are different than for denitrification (Rysgaard and Glud, 2004). Estuarine sediments are sites of intense organic matter remineralization, which can yield high concentrations of NO_3^- and NH_4^+ (Blackburn and Henriksen, 1983; Nowicki and Nixon, 1985)—the required substrates for anammox. Other processes, such as Mn(II) oxidation by NO_3^- or Mn(IV) reduction by NH_4^+ (Luther et al., 1997), can also result in the evolution of N_2 in suboxic sediments. Thus, anammox is likely to occur in many estuarine systems.

Denitrification, also known as *dissimilatory NO_3^- or NO_2^- reduction*, is the reduction of NO_3^- or NO_2^- to any gaseous form of N such as NO, N_2O, and N_2 by microorganisms, as in the case of N_2 production shown below:

$$CH_2O + NO_3^- + 2H^+ \rightarrow CO_2 + 1/2N_2 + 2H_2O \quad (3.23)$$
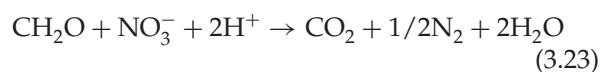
The denitrification pathway involves the production of intermediates such as NO_2^-, NO, and N_2O. Numerous methods on how to measure denitrification have been developed in recent years ranging from acetylene inhibition (Sørensen, 1978), labeled N tracers (Nishio et al., 1982; Rysgaard et al., 1993), direct N_2 flux measurements (Seitzinger et al., 1980; Nowicki, 1994), water column and sediment changes in N_2 (Devol, 1991), to core and chamber incubation with N isotopes (Nielsen, 1992)—more details on comparisons of these methods are provided in LaMontagne and Valiela (1995). Denitrification represents the major pathway from which N is lost from estuaries and has been shown to be proportional to the log mean water residence time ($r^2 = 0.75$), across a range of rivers and estuaries, suggests that with increasing residence time, N will be recycled in the water column and sediments more extensively resulting in greater denitrification (Nixon et al., 1996; Fig. 3.12).

In general, NO_3^- reduction produced N_2, which reduces the total availability of N in a system
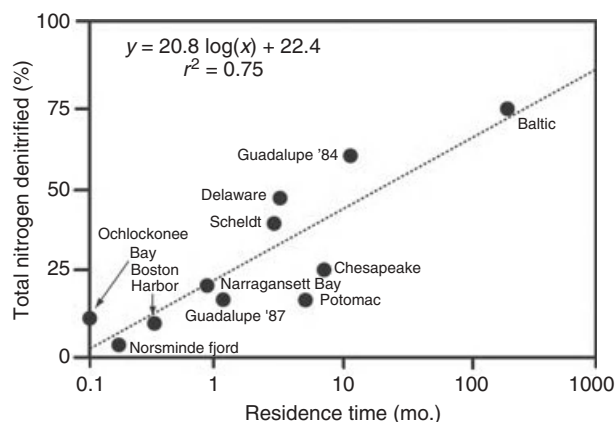
FIGURE 3.12 Fraction (%) of total N input from land and atmosphere that is denitrified in different estuaries as a function of residence time (months). *Source:* Modified from Nixon et al. (1996).

(Howarth et al., 1988a,b). However, if another pathway of *dissimilatory NO_3^- reduction to NH_4^+* (DNRA) is taken, it is found that N will be retained in a system, thereby increasing the total available N for organisms (Koike and Hattori, 1978; Jørgensen, 1989; Patrick et al., 1996). Although very little is known about the ecological consequences of DNRA (Sørensen, 1987; Cornwell et al., 1999), rates of DNRA can be as high as denitrification in shallow estuaries and tidal flats (Bonin et al., 1998; Tobias et al., 2001). Recent work in Laguna Madre/Baffin Bay (USA) has shown that while sulfides can inhibit denitrification, they may stimulate DNRA by providing an electron donor; this likely results in the retention of available N in estuaries (An and Gardner, 2002). Studies have reported the existence of chemolithotrophic bacteria that use sulfur compounds as an electron donor to convert NO_3^- to NH_4^+ (Schedel and Truper, 1980).

Assimilation of DON involves the uptake and incorporation of organic forms of N, such as amino acids, into biomass by both heterotrophic and autotrophic organisms. The DON pool represents an important component of the N cycle in estuarine systems (Sharp, 1983; Jackson and Williams, 1985), with a diverse range of sources and sinks (Bronk and Ward, 2000; Bronk, 2002). However, much of the work to date has focused on DIN loading to estuaries. Increases in loading of DIN to estuaries have also been accompanied by increases in DON (Correll and Ford, 1982). In fact, rivers that are a critical source of N to estuaries can have over 80% of their total N represented as DON (Meybeck, 1982; Seitzinger and Sanders, 1997, Bronk, 2002). The major ''sinks'' or pathways of DON consumption are mediated by

bacteria (Anita et al., 1991; Bronk, 2002), archaea (Ouverney and Fuhrman, 2000), and to a lesser degree protists (Tranvik et al., 1993). Phytoplankton can also use some DON compounds. The production of organic N *de novo* from DIN by bacteria as well as the fixation of atmospheric N_2 is evidence for the importance of particulate heterotrophic organic N in aquatic systems (Kirchman, 1994).

3.5.3 Sediment–Water Exchange of Dissolved Nitrogen

Estuarine and coastal sediments are important environments for the bacterial remineralization of nutrients (Rowe et al., 1975; Nixon, 1981; Boynton et al., 1982; Blackburn and Henriksen, 1983; Nowicki and Nixon, 1985; Sundback et al., 1991; Warnken et al., 2000) that also support neritic production—via fluxes across the sediment–water interface (Cowan and Boynton, 1996). The rates of remineralization and nutrient fluxes are typically highest with increasing water temperatures (Hargrave, 1969; Kemp and Boynton, 1984). Many other factors, such as redox status of the sediments and overlying water column, sorption/desorption processes, microbial respiration, and macromeiobenthic excretion, contribute to variability of sediment–water exchange of nutrients (Kemp and Boynton, 1981; Cowan and Boynton, 1996).

The major pathways of the N cycle in sediments are strongly influenced by the redox conditions in bottom waters and sediments (Fig. 3.13). Both diffusive and advective processes strongly control the distribution of O and N compounds, which ultimately affect the coupling between nitrification and denitrification (Jørgensen and Boudreau, 2001). For example, anaerobic degradation of N-containing organic matter will contribute to the formation of DON and NH_4^+ (ammonification), which can then either efflux to the water column or be oxidized to NO_2^- and NO_3^- (nitrification). Depending on the diffusive gradient, NO_3^- may also move downward where it can support denitrification just below the oxic–anoxic interface in sediments (Fig. 3.13; Kristensen, 1988; Rysgaard et al., 1994). Experimental loading of N in sediments showed that moderate loading increased N removal via denitrification but decreased rates of denitrification at high N loading (Sloth et al., 1995). The incorporation and/or loss of NO_3^- from sediments will also be dependent on the presence and type of bioturbation (Aller, 2001). Ammonium also accounts for most of the DIN secreted by invertebrates, as an end-product of protein catabolism (Le Bornge, 1986).

Estuaries are active sites of nitrous oxide (N_2O) production (Bange et al., 1996; Seitzinger and Kroeze,

(a)

(b)
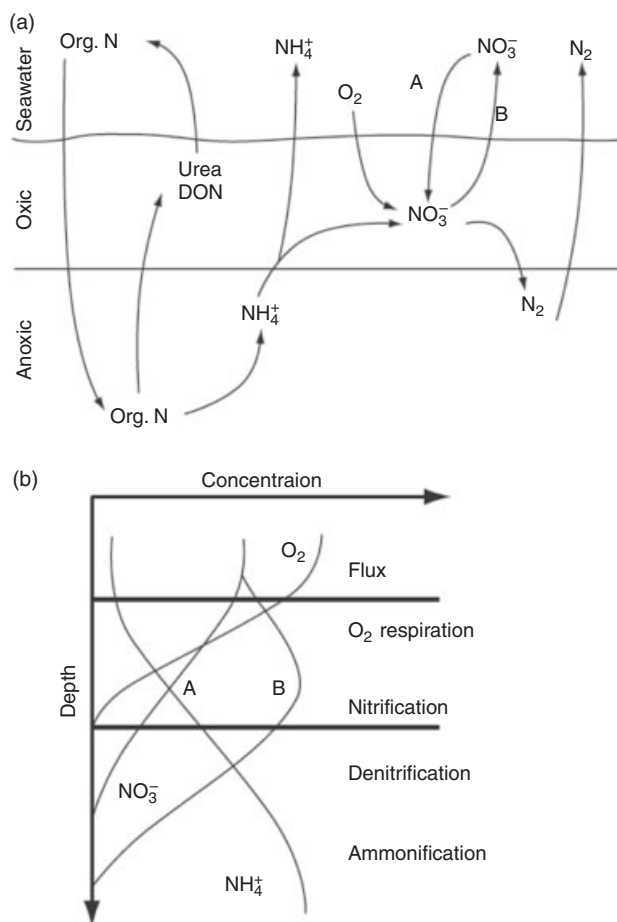
FIGURE 3.13 Major pathways of the N cycle in sediments (a) and as a function of redox conditions in bottom waters and sediments (b). Both diffusive and advective processes strongly control the distribution of O and N compounds, which ultimately affect the coupling between nitrification and denitrification. *Source:* Modified from Jørgensen and Boudreau (2001).

1998; Usui et al., 2001; Bauza et al., 2002). Nitrous oxide is one of the major greenhouse gases in the Earth's atmosphere (Wang et al., 1976; Khalil and Rasmussen, 1992). In fact, the Global Warming Potential of N_2O (310) is considerably higher than that of CO_2 (1) (Houghton et al., 1995). Furthermore, N_2O also plays a role in stratospheric ozone depletion (Hahn and Crutzen, 1982). Enhanced nutrient loading to estuaries stimulates microbial processes that include N_2O production (Seitzinger and Nixon, 1985; Seitzinger, 1988; Seitzinger and Kroeze, 1998; Usui et al., 2001). Chemoautotrophic nitrification and denitrification are the primary processes that produce N_2O in natural systems (Yoshinari, 1990). Estuarine sediments are characterized by high spatial and temporal variability in N_2O production (Middelburg et al., 1995; Usui et al., 2001).

3.5.4 Sources of Phosphorus to Estuaries

Phosphorus (P) is one of the best-studied nutrients in aquatic ecosystems because of its role in limiting primary production on ecological and geological timescales (van Capellen and Ingall, 1996). Other key linkages to biological systems include the role of P as an essential constituent of genetic material (RNA and DNA), cellular membranes (phospholipids), as well as in energy transforming molecules (e.g., ATP). Consequently, marine P has received considerable attention in recent decades, with particular emphasis on source and sink terms in budgets (Froelich et al., 1982; Meybeck, 1982; Sutula et al., 2004). Excessive loading of N to estuarine waters can result in P limitation in systems that are generally considered to be N limited. In such cases where primary production is limited by P, N:P ratios are expected to exceed the Redfield value of 16:1 but can be replenished by sediment efflux of P due to redox changes.

The cycling and availability of P in estuaries is largely dependent on P speciation. Consequently, total P (TP) has traditionally been divided into *total dissolved P* (TDP) and *total particulate P* (TPP) fractions (Juday et al., 1927), which can further be divided into *dissolved* and *particulate organic P* (DOP and POP) and *dissolved* and *particulate inorganic P* (DIP and PIP) pools. Another defined fraction within the TP pool is *reactive phosphorus*, which has been used to describe the *potentially bioavailable P* (Duce et al., 1991; Delaney, 1998). Much of the work to date has focused on the *soluble reactive P* (SRP), which is characterized as the P fraction that forms a phosphomolybdate complex under acidic conditions (Strickland and Parsons, 1972). A significant fraction of the SRP comprises *orthophosphate* ($H_2PO_4^-$) and acid-labile organic compounds such as simple phosphate sugars (McKelvie et al., 1995). The DIP fraction is composed of phosphate (PO_4^-), phosphoric acid (HPO_4^{2-}), orthophosphate ($H_2PO_4^-$), and triprotic phosphoric acid (H_3PO_4); dissociation constants in freshwater and seawater are shown in Table 3.5 (Atlas, 1975; Stumm and Morgan, 1981).

The relative abundance of these species will vary with pH in aquatic systems making $H_2PO_4^-$ and HPO_4^{2-} the more common species in freshwater and seawater, respectively (Fig. 3.14; Morel, 1983). The difference between TDP and SRP provides an estimate of the DOP pool, which has more recently been referred to as *soluble nonreactive P* (Benitez-Nelson and Karl, 2002). This can represent a much larger pool than SRP and can also be an important source of P to oceanic organisms (Benitez-Nelson and Karl, 2002).

TABLE 3.5 **Dissociation constants of phosphoric acid at 25 °C**

	Distilled Water[a]	Seawater[b]
$H_3PO_4 \leftrightarrow H^+ + H_2PO_4^-$	2.2	1.6
$H_2PO_4^- \leftrightarrow H^+ + HPO_4^{2-}$	7.2	6.1
$HPO_4^{2-} \leftrightarrow H^+ + PO_4^{3-}$	12.3	8.6

[a]Stumm and Morgan (1981).
[b]Atlas (1975).
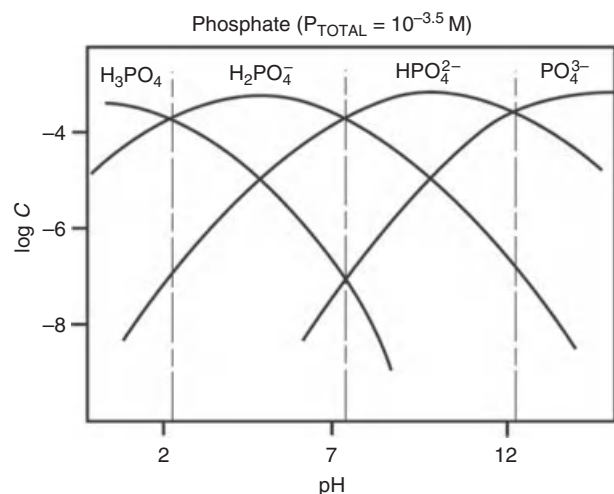
FIGURE 3.14 Relative abundance of these different dissolved inorganic P compounds as a function of pH in aquatic systems; $H_2PO_4^-$ and HPO_4^{2-} are the more common species in freshwater and seawater, respectively. *Source: Modified from Morel (1983).*

Using ^{31}P nuclear magnetic resonance (NMR) spectroscopy, the dominant groups of P found in dissolved organic phosphorus (DOP) in oceanic systems are phosphonates, phosphate monoesters, orthophosphate, phosphate diesters, pyrophosphates, and tri- and tetrapolyphosphates (Clark et al., 1998; Kolowith et al., 2001), and very little work on this topic has been performed in river/estuarine systems. It should be noted that phosphonates are a group of compounds that have a C=P bond, often associated with phosphoproteins (Quin, 1967) and phospholipids (Hori et al., 1984).

Rivers are the major source of P to the ocean, via estuaries, where major chemical and biological transformations of P occur before it is delivered to the ocean (Froelich et al., 1982; Conley et al., 1995). The major source of P to rivers is from weathering of rock materials, and this is the major pathway from which P is lost from terrestrial systems (Jahnke, 2000). Phosphorus is the tenth most abundant element on Earth with an average crustal abundance of 0.1%

(Jahnke, 2000). Apatite is the most abundant phosphate mineral in the Earth's crust, representing more than 95% of all the crustal P. Thus, the yield of P from weathering processes will vary depending on the rock type. For example, P is generally low in granites (e.g., 0.13–0.27%), higher in shales (0.15–0.40%), and highest in basalts (0.40–0.80%; Kornitnig, 1978). The fact that the uptake of P into organic matter per year is greater than the amount lost by land or supplied by rivers emphasizes the importance of P recycling in natural systems (Berner and Berner, 1996).

Inputs of atmospheric sources of P are generally considered to be insignificant to coastal systems. In fact, they represent less than 10% of the riverine flux of reactive P (Duce et al., 1991; Delaney, 1998). Only in highly oligotrophic systems, such as oceanic gyres and the eastern Mediterranean (Krom et al., 1991, 1992), can such inputs have a significant impact on primary production. In fact, atmospheric deposition of DIP may account for as much as 38% of the new production during summer and spring in the Levantine Basin, eastern Mediterranean (Markaki et al., 2003). While gaseous forms of N and S are important components of natural systems, no significant quantities of any stable gaseous forms of P have been found in aquatic systems.

## 3.5.5 Phosphorus Fluxes Across the Sediment–Water Interface

The release of P from estuarine sediments is a common and important process that varies spatially and temporally. Early studies showed, using *in situ* benthic flux chambers, that P fluxes ranged from 30 to 230 mg $P/m^2/$ day in estuaries such as Narragansett Bay (USA; Elderfield et al., 1981a, 1981b), Potomac River estuary (USA; Callender and Hammond, 1982), San Franciso Bay (USA; Hammond et al., 1985), and Guadalupe Bay (USA; Montagna, 1989). Another key factor controlling the release of P from sediments is temperature. In many temperate systems, for example, much of the regeneration of P in sediments occurs via microbial processes, which are typically highest in summer months. Similarly, another fundamental pattern involving P release from sediments is that it decreases with increasing salinity. Spatial variability in the extent of subtidal and intertidal areas may also have an impact on the spatiotemporal variability in P concentrations.

Numerous studies in freshwater (e.g., Roden and Edmonds, 1997; Hupfer et al., 2004) and marine (e.g., Sundby et al., 1992; Gunnars and Blomqvist, 1997; Sutula et al., 2004) systems have examined mechanisms controlling the release and efflux of P from sediments. Since total sediment P does not reflect

exchange capacity or bioavailability of P, sequential chemical extraction techniques have been useful in separating out different pools of P (Ruttenberg, 1992; Jensen and Thamdrup, 1993). Sedimentary pools of P have generally been divided into the following fractions: (i) organic P, (ii) Fe-bound P, (iii) *authigenic P minerals* (e.g., carbonate fluoroapatite, struvite, and vivianite), and (iv) *detrital P minerals* (e.g., feldspar; Ruttenberg and Berner, 1993). More specifically, it is the organic P (Ingall and Jahnke, 1997) and Fe-bound P (Krom and Berner, 1981) fractions that are considered to be the most reactive and most likely to be released from sediments during P regeneration. While it is generally accepted that much of the inorganic P is bound with Fe and Ca in sediments, the condition of the organic fraction is less clear. Some of the organic P components occur as phytic acid, nucleic acids, and humic substances (Ogram et al., 1978; de Groot, 1990). In the case of organic P release, PO_4^{3-} is remineralized during diagenesis of organic matter. In the Fe-bound fraction of P, release of P can occur from Fe oxides as sediments become reduced under anaerobic conditions (McManus et al., 1997). Other experimental work has shown that P released from estuarine and freshwater sediments was largely controlled by the reduction of FeOOH (Gunnars and Blomqvist, 1997). Thus, the degree to which P is released through both these pathways is further controlled by stability of redox conditions as well as the extent of authigenic P mineral formation. For example, dissolved inorganic phosphorus in bottom waters was shown to be negatively correlated with oxygen concentration, indicating the release of DIP from sediments in the Baltic Sea (Fig. 3.15; Conley, 2002).

When compared with freshwater systems, interactions between Fe and S (Canfield, 1989; Kostka and Luther, 1995) in marine and estuarine systems can further complicate the mechanisms controlling P release. For example, experimental work by Gunnars and Blomqvist (1997) indicated that the reduction of FeOOH was most important in controlling the release and efflux of PO_4^{3-} across the sediment–water interface. Moreover, it was found that the dissolved Fe:P ratio of the efflux was equal to 1 in freshwater sediments but less than 1 in marine sediments. It was further shown that carbon-normalized P remobilization from sediments was approximately fivefold higher in marine systems with higher SO_4^{2-} concentrations than in freshwater systems with low SO_4^{2-} concentrations (Caraco et al., 1990). These differences in ratios are likely explained by quick scavenging of Fe^{2+} by Fe sulfides in marine and estuarine systems, which can result in the precipitation of FeS and FeS_2 (pyrite; Taillefert et al., 2000).
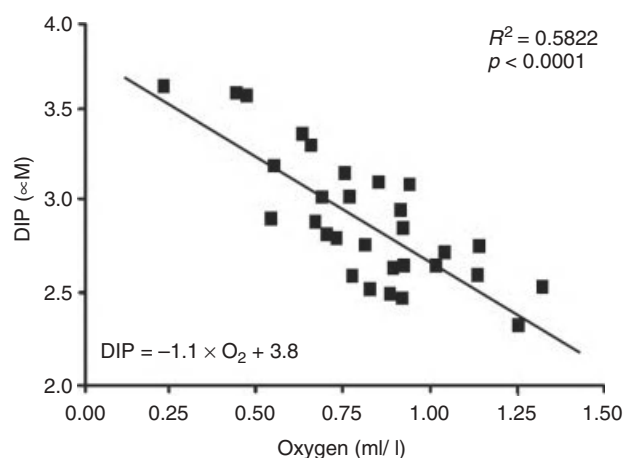
FIGURE 3.15 Negative correlations between dissolved inorganic phosphorus (μM) and oxygen (ml/l) concentrations in bottom waters of the Baltic Sea. *Source:* Modified from Conley (2002).

3.5.6 Cycling of Inorganic and Organic Phosphorus

In both freshwater and estuarine systems, concentrations of DIP has also been strongly linked with the suspended sediment load. In fact, a stable or "equilibrium" concentration range of DIP, between 0.5 and 2 μM, has been reported for a number of estuarine systems (Liss, 1976; Froelich, 1988; Ormaza-Gonzalez and Statham, 1991). These stable DIP concentrations are believed to be controlled by a "buffering" of DIP through the adsorption and desorption onto metal oxide surfaces (Mortimer, 1941; Carritt and Goodgal, 1954; Stirling and Wormald, 1977). This "P-buffering" is believed to balance the low availability of SRP in higher salinity waters, which occurs from phytoplankton uptake and anionic competition for surface adsorption sites (Froelich, 1988; Fox, 1989). For example, TPP concentration decreases with increasing salinity in the Delaware Bay (Lebo, 1991) and Sheldt (the Netherlands) estuaries, suggesting the importance of desorption of DIP from aluminum and iron oxides. Finally, in the high salinity reaches of estuaries, calcite can serve as a carrier phase for adsorbed P (de Jonge and Villerius, 1989). However, another work has shown that inorganic exchange processes were not able to "buffer" DIP concentrations across different regions of Chesapeake Bay (Conley et al., 1995). When examining the ratio of Fe:P in citrate–dithionate–bicarbonate (CDB-P) extracts in surface and bottom samples of suspended particles, there is a clear decrease in the ratio with increasing salinity (Conley et al., 1995). This decrease in

CBD-Fe:P has also been observed in the St Lawrence estuary (Canada; Lucotte and d'Anglejan, 1983).

Another geochemical/physical mechanism controlling the P concentrations in estuarine waters may involve particle sorting and/or particle colloid interactions. For example, negative correlations were found between particulate P and SPM and the partition coefficient (K_d) for orthophosphate ($K_d = [TPP]$ [mg/kg]/[orthophosphate] [mg/l]) and SPM in the Galveston estuary (USA; Santschi, 1995). Much of the TP in this system is composed of orthophosphate as indicated by the strong positive relationship between orthophosphate and TP. The negative correlation between K_d and SPM is commonly referred to as the *particle concentration effect,* an effect well supported by radionuclide and trace metal work (e.g., Honeyman and Santschi, 1988; Baskaran et al., 1992; Benoit et al., 1994). This effect occurs when a fraction of the P, or trace elements and radionuclides, is associated with the colloidal fraction, which is less than 0.45 µm and greater than 1 kD (Benoit et al., 1994). In fact, the colloidal P represented 30–80% of the filter-passing organic P concentration, an amount significant enough to account for such an effect.

Although the characterization of DOP in rivers and estuaries has been largely ignored, some work in the Mississippi River indicated that the composition of soluble nonreactive P primarily consisted of diester and monoester phosphate, phosphonates, orthophosphates, and/or tri and tetrapolyphosphates (Nanny and Minear, 1997)—essentially the same as that found in the ocean (Kolowith et al., 2001). Phosphonates and refractory P esters are also abundant in marine sediments and may represent a significant sink for organic P (Ingall et al., 1990). Conversely, recent work has shown that phosphonates may actually be preferentially removed relative to other bioavailable P esters, in anoxic waters (Benitez-Nelson et al., 2004). From the perspective of soil inputs at the river end-member of estuaries, 90% of the total organic P in some soils was represented in the form of the monoester phosphate fraction (Condron et al., 1985), with phosphonates also being present (Hawkes et al., 1984). These comparisons of possible oceanic and terrigenous end-member inputs to estuaries provide at least some insight on the potential composition of DOP in estuaries.

3.5.7 Sources of Silica to Estuaries

Although silicon (Si) is the second most abundant element in the Earth's crust, it has relatively limited importance to biogeochemical cycles (Conley, 2002; Ragueneau et al., 2006a,b). Much of the work to date has focused on the weathering of Si (Wollast and Mackenzie, 1983) and the oceanic Si cycle (DeMaster, 1981; Tréguer et al., 1995). Only recently has the cycling of Si in terrestrial ecosystems been shown to be important on a global scale (Conley, 2002). The majority of inputs to the oceans occur via rivers (80%), with much of the losses controlled by sedimentation of biogenic silica or opal (Tréguer et al., 1995). The average global concentration of dissolved SiO_2 (DSi) in rivers is 150 µm/l (Conley, 1997); the majority of this DSi is in the form of silicic acid (H_4SiO_4) in rivers, which typically have a pH in the range of 7.3–8.0.

The primary source of DSi (80%) to the global ocean, via estuaries, is riverine. However, anthropogenic alterations have begun to change to abundance and sources of riverine Si (Tréguer et al., 1995; Conley, 2002). For example, decreases in the delivery of DSi loading of Mississippi River to coastal waters were attributed to enhanced N loading to the river, which is believed to have increased diatom production and sedimentation in the watershed (Turner and Rabalais, 1991; Turner et al., 2003). However, increases in the number of dams can also account for such decreases (Conley et al., 1993). Decreases in DSi in the Danube River (Humborg et al., 1997) and the Swedish rivers (Humborg et al., 2000, 2002) have also been attributed to enhanced uptake of DSi from enhanced diatom production.

Other less important sources of DSi to estuaries and the coastal ocean include SGD, atmospheric inputs, and in the case of estuaries, import of DSi from coastal upwelling (Ragueneau et al., 2006a,b). For SGD, current estimates of the global flux range from 0.01% to 10% of surface runoff (Taniguchi et al., 2002). More work is needed on DSi in groundwaters before any conclusive statements can be made about its effects on estuarine biogeochemistry. As for atmospheric inputs of Si, fluxes to the global ocean have been estimated to be approximately 0.5 Tmol Si/year (Duce et al., 1991), although these inputs only account for 0.2% of the annual oceanic gross biogenic Si production and 10% of the river inputs.

3.5.8 Cycling of Silica

Temporal and spatial variability in the annual cycles of DSi in estuaries primarily change as a function of river inputs and biological uptake. In Chesapeake Bay, sources of DSi in winter and spring were primarily from river inputs (Fig. 3.16; Conley and Malone, 1992). The variability in the maxima and minima of DSi decreased from the head to the mouth of the estuary, due to reduced linkages with freshwater inputs. In summer months, a significant fraction of DSi was supplied from benthic regeneration. The highest concentrations of DSi in bottom waters of the

bay occurred in the summer because biogenic Si dissolution is strongly temperature dependent (Kamatani, 1982). Much of the diatom demand for DSi can be supported by flux of this regenerated Si in sediments to the water column in Chesapeake Bay (D'Elia et al., 1983). From a spatial perspective, the highest DSi concentrations occurred in bottom waters in the mesohaline and lower bay regions—where regeneration rates were highest. However, maximum uptake rates of DSi by diatoms also occurred in the mesohaline region in spring—resulting in significant DSi limitation (Fig. 3.16; Conley and Malone, 1992).

3.5.9 Sources of Sulfur to Estuaries

Sulfur (S) is an important redox element in estuaries because of its linkage with biogeochemical processes such as SO_4^{2-} reduction (Howarth and Teal, 1979; Luther et al., 1986; Roden and Tuttle, 1993a, 1993b), pyrite (FeS_2) formation (Giblin, 1988; Hsieh and Yang, 1997), metal cycling (Tang et al., 2000), ecosystem energetics (King et al., 1982; Howes et al., 1984), and atmospheric S emissions (Dacey et al., 1987; Simo et al., 1997). The range of oxidations for S intermediates formed in each of these processes is between +VI and −II.

On a global scale, most of the S is located in the lithosphere; however, there are important interactions between the hydrosphere, biosphere, and atmosphere where important transfers of S occur (Charlson, 2000). For example, coal and biomass burning, along with volcano emissions inject SO_2 into the atmosphere, which can then be further oxidized in the atmosphere and removed as SO_4^{2-} in rainwater (Galloway, 1985). An example of biogenic sulfur formation is the reduction of seawater SO_4^{2-} to sulfide by phytoplankton and eventual incorporation of the S into dimethylsulfoniopropionate (DMSP). DMSP, in turn, is converted to volatile DMS (CH_3SCH_3), which is emitted to the atmosphere. In seawater, SO_4^{2-} represents one of the major ions, with concentrations that range from 24 to 28 mM, which is considerably higher than the concentrations found in freshwaters (~0.1 mM). This marked difference makes seawater the major input to estuaries and sets up an important gradient in estuarine biogeochemical cycling.

Approximately 50% of the global flux of S to the atmosphere is derived from marine emissions of DMS. Oxidation of DMS in the atmosphere leads to production of SO_4^{2-} aerosols, which can influence global climate patterns (Charlson et al., 1987; Andreae and Crutzen, 1997). The key processes controlling DMS emissions from the euphotic zone in the ocean are bacterial metabolism, water column mixing, and photochemistry (Kieber et al., 1996; Kiene and Linn,
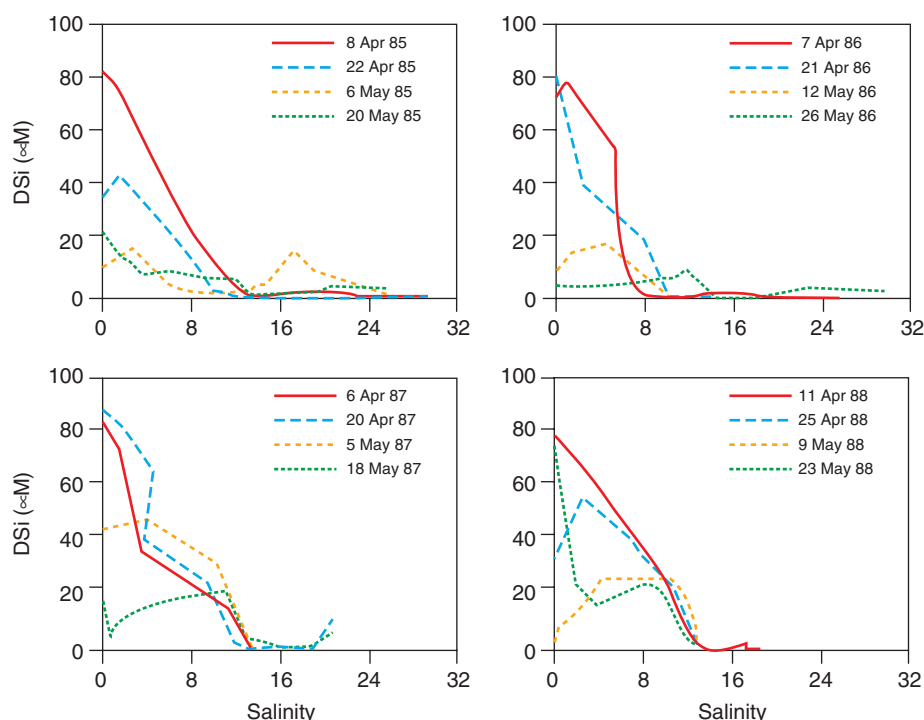
FIGURE 3.16 Temporal variability of concentrations of DSi (μM) in Chesapeake Bay across a salinity gradient. *Source:* Modified from Conley and Malone (1992).
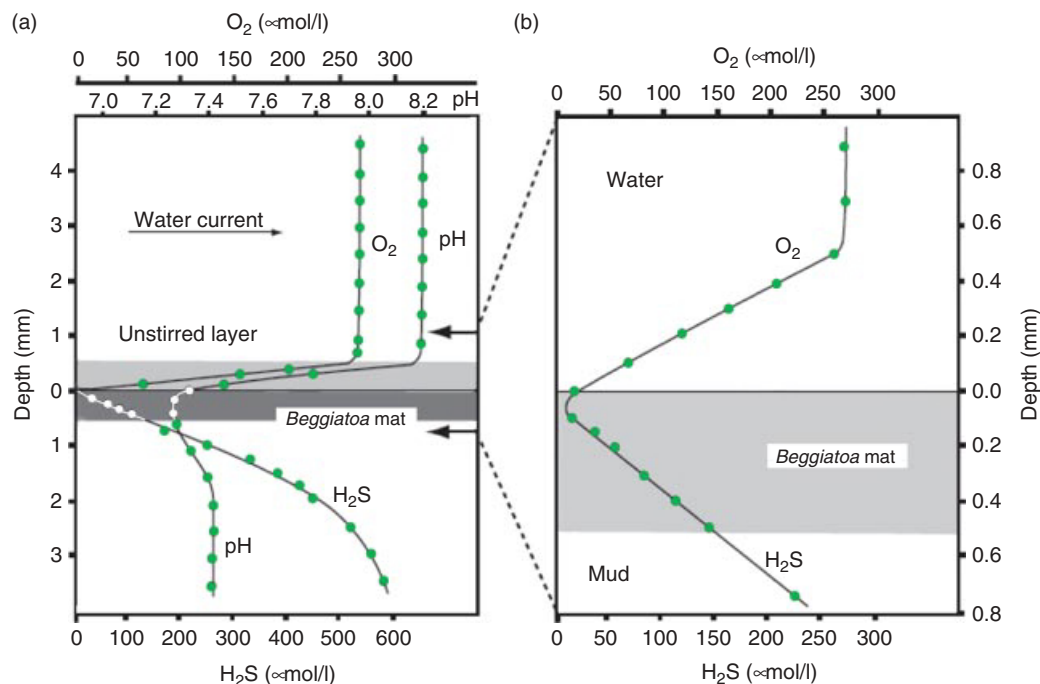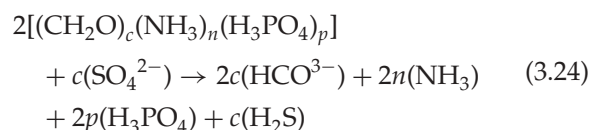
FIGURE 3.17 Depth profile of the microzone of O_2 and H_2S at the sediment–water interface (ca. 1–2 mm) where *Beggiatoa* spp. and *Thiovulum* spp. thrive. *Source:* Modified from Jørgensen and Revsbech (1983).

2000). The major precursor of DMS in the ocean is the algal osmolyte DMSP ($(CH_3)_2S^+CH_2CH_2COO^-$; Charlson et al., 1987; Dacey et al., 1987). DMS is formed by enzymatic cleavage of DMSP (Kiene, 1990). The release of dissolved DMSP (DMSPd) occurs from direct excretion, viral lysis, and grazing processes (Dacey and Wakeham, 1986; Malin et al., 1998). Once released, bacterioplankton can metabolize DMSPd where it can be converted to sulfate, DMS, and methanethiol (MeSH; CH_3SH; Kiene and Linn, 2000).

3.5.10 Cycling of Inorganic and Organic Sulfur in Estuarine Sediments

Anaerobic sediment metabolism represents a significant pathway for carbon cycling in estuarine sediments (Jørgensen, 1977, 1982; Crill and Martens, 1987; Roden and Tuttle, 1992). In particular, SO_4^{2-} *reduction* (SR) is the terminal microbial respiration process in anaerobic sediments, when SO_4^{2-} is not limiting, leading to the formation of hydrogen sulfide (H_2S; Capone and Kiene, 1988). Sulfate reduction is particularly important in the S and C chemistry of highly productive shallow-water subtidal and salt marsh environments (Howarth and Teal, 1979; King et al., 1985; Kostka and Luther, 1994). In fact, some SO_4^{2-} reducing bacteria (SRB) are closely associated with the

rhizosphere of *S. alterniflora*, an interaction that is critical in controlling biogeochemical cycling in marsh sediments (Hines et al., 1989). Some of the dominant SRB genera within the families of Desufovibrionaceae and Desulfobacteriaceae are *Desulfovibrio desulfuricans, Desulfobulbus propionicus, Desulfobacter* spp., *Desulfococcus multivorans, Desulfosarcina variabilis*, and *Desulfobacterium* spp. (Rooney-Varga et al., 1997; King et al., 2000). Some of these SRB are also important in methyl mercury (CH_3Hg) formation in contaminated sediments. Sources of S to sediments are SO_4^{2-} and detrital sulfur inputs to the sediment–water interface. Organic matter decomposition via sulfate reduction can be represented by the following equation (Richards, 1965; Lord and Church, 1983):

$$2[(CH_2O)_c(NH_3)_n(H_3PO_4)_p]$$
$$+ c(SO_4^{2-}) \rightarrow 2c(HCO^{3-}) + 2n(NH_3) \quad (3.24)$$
$$+ 2p(H_3PO_4) + c(H_2S)$$

where c, n, and p represent the C:N:P ratio of the decomposing organic matter.

A significant fraction of the sulfides formed by sulfate reduction are reoxidized to SO_4^{2-} at the oxic–anoxic interface in sediments. Dissolved sulfides (DS; $DS = S^{2-} + HS^- + H_2S$) formed in porewaters during sulfate reduction can diffuse into overlying

bottom waters and contribute to O_2 depletion in estuaries (Tuttle et al., 1987). Sulfides can also be removed from porewaters via reactions with Fe oxyhydroxides to form pyrite (FeS$_2$; Berner, 1970, 1984). In addition to vertical molecular diffusion as a controlling factor in the DS transport, gas bubble ebullition, derived from CH_4 production beneath the sulfate reduction zone, can be important in stripping DS from porewaters (Roden and Tuttle, 1992). Although sulfate reduction has been viewed as the dominant pathway of organic matter oxidation in anaerobic salt marsh sediments (see reviews by Howarth, 1993), another work has suggested that microbial Fe(III) reduction (FeR) is also key in controlling the oxidation of organic C in these sediments and is inherently linked with DS formed from SR (Kostka and Luther, 1995).
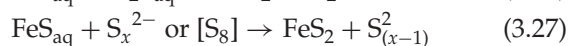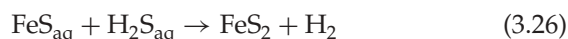
The flux of DS across the sediment–water interface can in some cases be strongly influenced by the presence of chemoautotrophic bacterial mats in estuaries. These sulfur oxidizing bacteria occur at the oxic–anoxic interface. The dominant colorless bacteria that live within the microzone of the O_2 and H_2S interface (ca. 1–2 mm) are *Beggiatoa* and *Thiovulum* spp. (Jørgensen and Revsbech, 1983; Jørgensen and Des Marais, 1986). This early work demonstrated through the use of microelectrodes that these bacteria live within the microgradiant of O_2 and H_2S (Fig. 3.17; Jørgensen and Revsbech, 1983). The steep H_2S and O_2 gradient typically occurs between 0 and 0.5 mm. In the presence of O_2, these bacteria can oxidize H_2S to S^0, which can be further oxidized to SO_4^{2-} (Nelson and Castenholz, 1981). These bacteria enzymatically oxidize H_2S in the presence of O_2—despite rapid abiotic oxidation of H_2S. The common pigmented sulfur bacteria are the green sulfur bacteria (GSB; e.g., *Prosthecochloris aestuarii*), which are obligate anaerobes that use H_2S as the dominant electron acceptor for *photolithoautotrophy* (Massé et al., 2002). These GSB are commonly found in occurrence with brown colored GSB (e.g., *Chlorobium vibriforme*) in brackish to hypersaline environments.

In sediments, Fe sulfides are typically divided into the following two groups: *acid volatile sulfides* (AVSs), which are evolved via acid distillation and generally include amorphous forms (e.g., mackinawite [FeS], greigite [Fe$_3$S$_4$], and pyrrhotite [FeS]; Morse and Cornwell, 1987). In some cases, AVS may represent the dominant pool of sulfides in estuarine sediments (Oenema, 1990). Pyrite (FeS$_2$) is the dominant Fe–sulfur mineral in most estuarine systems, particularly in salt marsh sediments (Hsieh and Yang, 1997). In sediments with high concentrations of sulfide, reductive dissolution of Fe(III) oxyhydroxide phases results in the formation of FeS$_{aq}$ and FeS$_s$ as

shown below:

$$Fe^{2+} + HS^- \rightarrow H^+ + FeS_{aq} \qquad (3.25)$$
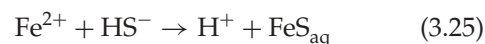
Pyritization can then occur under anoxic conditions relatively quickly by reaction of H_2S and S(0) (as S_8 or polysulfides [S_x^{2-}]) with FeS—both aqueous and solid forms (Rickard and Luther, 1997; Rozan et al., 2002) in the following equations:

$$FeS_{aq} + H_2S_{aq} \rightarrow FeS_2 + H_2 \qquad (3.26)$$
$$FeS_{aq} + S_x^{2-} \text{ or } [S_8] \rightarrow FeS_2 + S_{(x-1)}^2 \qquad (3.27)$$

Pyrite is considered to be very stable under reducing conditions where it can be preserved over geological time, thereby retaining high amounts of energy (Howarth, 1984); however, under oxidizing conditions, FeS$_2$ decomposes rapidly. Although there can be considerable differences in the rates of pyritization of different precursor iron hydroxide minerals (Canfield et al., 1992; Raiswell and Canfield, 1996), the actual effects of mineralogy appear to only be important in the initial iron sulfidization and not in pyritization rates (Canfield et al., 1992; Morse and Wang, 1997).

The degree of pyritization (DP) is a parameter first used by Berner (1970) to distinguish environments where FeS$_2$ is Fe or carbon limited (Raiswell and Berner, 1985). It is a measure of the extent to which the original reducible or reactive Fe has been converted to FeS$_2$. The original equation defining DP has been modified in recent years because of the operational definition of reactive nonsulfidic Fe. The following equation incorporates some of these modifications and has been recently used by Rozan et al. (2002):

$$DP = \frac{[FeS_2]}{([FeS_2] + [AVS - Fe] + [dithionite - Fe])} \qquad (3.28)$$

where FeS$_2$ is the concentration of reduced S as pyrite, AVS, the acid volatile sulfur composed of both aqueous and solid FeS, dithionite $-$ Fe, the measure of nonsulfidic Fe.

3.5.11 Cycling of Inorganic and Organic Sulfur in Estuarine Waters

The emergence of DS from sediments into stratified bottom waters can contribute significantly to bottom water oxygen depletion in estuaries (Tuttle et al., 1987; Roden and Tuttle, 1992). Hydrogen sulfide's toxicity stems from its ability to combine with the Fe-heme of blood cells, thereby replacing O_2 and inhibiting respiration (Smith et al., 1977). The persistence and concentrations of H_2S in the bottom waters of estuaries are

controlled by many factors such as soluble reactive phosphorus (SRR), which is affected by organic matter/nutrient loading, temperature, and parameters controlling the flux of H_2S across the sediment–water interface and the transfer to surface waters (e.g., diffusive/advective processes and S-oxidizing bacteria).

Although there have only been a few studies to date, it has been suggested that coastal plumes (Turner et al., 1996; Simo et al., 1997) and estuaries (Iverson et al., 1989; Cerqueira and Pio, 1999) may be important atmospheric sources of DMS. DMS, a compound produced by certain phytoplankton, has possible implications on climate control once released into the atmosphere (Charlson et al., 1987). DMS is formed by cleavage of DMSP (Kiene, 1990). In fact, DMSP may provide as much as 100% of the sulfur and 3.4% of the carbon required for bacterial growth in oceanic waters (Kiene and Linn, 2000). Other sulfur compounds such as carbonyl sulfide (OCS) and carbon disulfide (CS_2) are also possible sources of S in estuaries.

3.5.12 Carbon Cycling in Estuaries

As discussed earlier, carbon dioxide water-to-air fluxes are significant in estuaries (Frankignoulle and Borges, 2001; Wang and Cai, 2004; Bianchi, 2007; Bauer and Bianchi, ; Bianchi and Bauer,). Estuaries and their associated marshes along the southeastern USA have received considerable attention on this topic (Cai and Wang, 1998; Cai et al., 2003; Wang and Cai, 2004). Calculated values of the partial pressure of CO_2 (pCO_2), based on dissolved inorganic carbon (DIC) and pH data, showed the highest pCO_2 (1000 to >6000 μatm) at the lowest salinities (<10) in estuarine waters of the Satilla and Altamaha Rivers (USA; Cai and Wang, 1998). Corresponding CO_2 water-to-air fluxes in these low salinity waters ranged from 20 to greater than 250 mol/m^2/ year. The high pCO_2 and CO_2 water-to-air fluxes in the Satilla and Altamaha rivers were attributed to inputs from organic carbon respiration in the tidally flooded salt marshes and groundwater (Cai and Wang, 1998). Recent work has shown the pCO_2 of groundwater entering the South Atlantic Bight (southeastern coast of USA) to be high (0.05–0.12 atm; Cai et al., 2003). This is consistent with other work, which suggests that the high pCO_2 in rivers is, in part, due to groundwater inputs (Kempe et al., 1991; Mook and Tan, 1991). More recently, export of DIC from marshes was found to rival that of riverine export to coastal waters of the South Atlantic Bight (Wang and Cai, 2004). This work further proposed that the pathway of CO_2 being fixed by marsh grasses and then exported to coastal waters in the form of

organic and inorganic carbon can be described as a "marsh CO_2 pump." Other studies have shown that marsh-influenced estuaries are important sources of DIC to adjacent coastal waters (Raymond et al., 2000; Neubauer and Anderson, 2003). Recent work also has documented the marsh pump in mangrove systems (Bouillon et al., 2003). Average pCO_2 for other estuarine systems in Europe and the United States indicate that estuaries are net sources of CO_2 to the atmosphere (Table 3.6). Highly dynamic regions in estuaries, such as the ETM, can be particularly important as net sources of CO_2 (Abril et al., 2004). While recent work has shown that estuarine plumes can be net sinks of CO_2, particularly in the outer plume region (Frankignoulle and Borges, 2001), overall estuarine systems are generally net sources (Borges and Franginoulle, 2002).

Methane is an important greenhouse gas in the atmosphere that has a mean concentration (1.7 ppm). While this is considerably lower than that of CO_2 (350 ppm), it has a greater *radiative forcing* capability (Cicerone and Oremland, 1988). Despite the smaller global surface area of estuaries relative to the global ocean, the contribution to total global CH_4 emission from estuaries (ca 7.4%) is within the range found for oceanic environments (1–10%; Bange et al., 1994). Recent water-to-air flux estimates indicate that estuaries contribute 1.1–3.0 Tg CH_4/ year to the global budget (Middelburg et al., 2002). Tidal creeks and marshes are the dominant source of CH_4 in estuaries (Middelburg et al., 2002). Groundwater also tends to be highly enriched in CH_4 (Bugna et al., 1996) and is likely responsible for the general increase in riverine CH_4 with increasing river size (Jones and Mulholland, 1998). Methane concentrations in rivers are typically one to two orders of magnitude higher than open ocean waters (Scranton and McShane, 1991; Jones and Amador, 1993; Middelburg et al., 2002). There exists a wide range of spatial and temporal variability in methane concentrations in rivers and estuaries (De Angelis and Scranton, 1993; Bianchi et al., 1996). Methane oxidation can be an important sink in estuaries as well and is highly dependent on temperature and salinity—with lower oxidation rates at higher salinities (De Angelis and Scranton, 1993; Pulliam, 1993). In fact, turnover of the dissolved CH_4 pool can occur as fast as 1.4–9 days in the upper Husdon River estuary (USA; De Angelis and Scranton, 1993) and less than 2 h to 1 day in the Ogeechee River (USA; Pulliam, 1993). In conclusion, there is considerable temporal and spatial variability in the sources and sinks of methane, water-to-air fluxes, as well as mechanisms

TABLE 3.6 Average pCO_2 ranges for various US and European estuaries[a]

Estuary	Number of Transects	Average pCO_2 Range (ppmv)
Altamaha (USA)[b]	1	380–7800
Scheldt (Belgium/Netherlands)[c]	10	496–6653
Sada (Portugal)[c]	1	575–5700
Satilla (USA)[b]	2	420–5475
Thames (UK)[c]	2	485–4900
Ems (Germany/Netherlands)[c]	1	560–3755
Gironde (France)[c]	5	499–3536
Douro (Portugal)[c]	1	1330–2200
York (USA)[d]	12	352–1896
Tamar (UK)[c]	2	390–1825
Hudson (NY, USA)[e]	6	517–1795
Rhine (Netherlands)[c]	3	563–1763
Rappahannock (USA)[d]	9	474–1613
James (USA)[d]	10	284–1361
Elbe (Germany)[c]	1	580–1100
Columbia (USA)[f]	1	590–950
Potomac (USA)[d]	12	646–878
Average		531–3129

[a]The average range was obtained by averaging the low and high concentrations for each transect, and the estuaries are ranked by the high average range.
[b]From Cai and Wang (1998) and Cai et al. (1999).
[c]From Frankignoulle et al. (1998).
[d]From Raymond et al. (2000).
[e]From Raymond et al. (1997).
[f]From Park et al. (1969).
Source: Modified from Raymond et al. (2000).

of transport (e.g., *ebullition, diffusion*, and *plant mediated*) in estuarine systems (Bianchi, 2007; Bauer and Bianchi, ; Bianchi and Bauer, , and references therein).

3.5.13 Transformations and Cycling of Dissolved and Particulate Organic Carbon (DOC and POC)

Sources of POC and DOC in estuaries consist of a diverse mixture of allochthonous and autochthonous sources. Hydraulic residence time, river discharge, tidal exchange, and frequency of resuspension events are, to name a few, important physical controlling variables that determine the fate and reactivity of organic carbon in estuaries. Once again, in this section, only a very brief overview of POC and DOC cycling dynamics in the waters and sediments of estuaries is provided, relying more on the background of organic carbon sources, chemical biomarkers, and

bulk isotopic measurements (Bianchi, 2007; Bauer and Bianchi, ; Bianchi and Bauer, , and references therein).

Concentrations of POC in many estuaries are strongly coupled with suspended sediment particulates, which may depend on river discharge and/or resuspension events. For example, in the Sabine–Neches estuary (USA), there is a significant increase in POC when total suspended particulates are lower than 20–30 mg/l (Fig. 3.18; Bianchi et al., 1997). This relationship has been found in large river systems; however, because of the higher suspended loads in many rivers, the increase in % POC of TOC typically occurs at less than 50 mg/l (Meybeck, 1982).

This general pattern is attributed to a dilution effect of sediment load on % POC at high river discharge and to an increase in phytoplankton production during high TSP and low light availability. Seasonal ranges of POC concentrations in San Francisco Bay and Chesapeake Bay estuaries are typical of many estuaries and are not significantly different between systems (Canuel, 2001). Seasonal and temporal differences in POC in both systems are generally controlled by river discharge and light availability. However, further analyses using fatty acid biomarkers reveals that phytoplankton represent a greater fraction of POC in Chesapeake Bay than in San Francisco Bay (Canuel, 2001). Thus, while bulk POC provides a general index of the overall loading of allochthonous and autochthonous C in the system, POC alone can be very misleading in terms of overall C cycling dynamics.
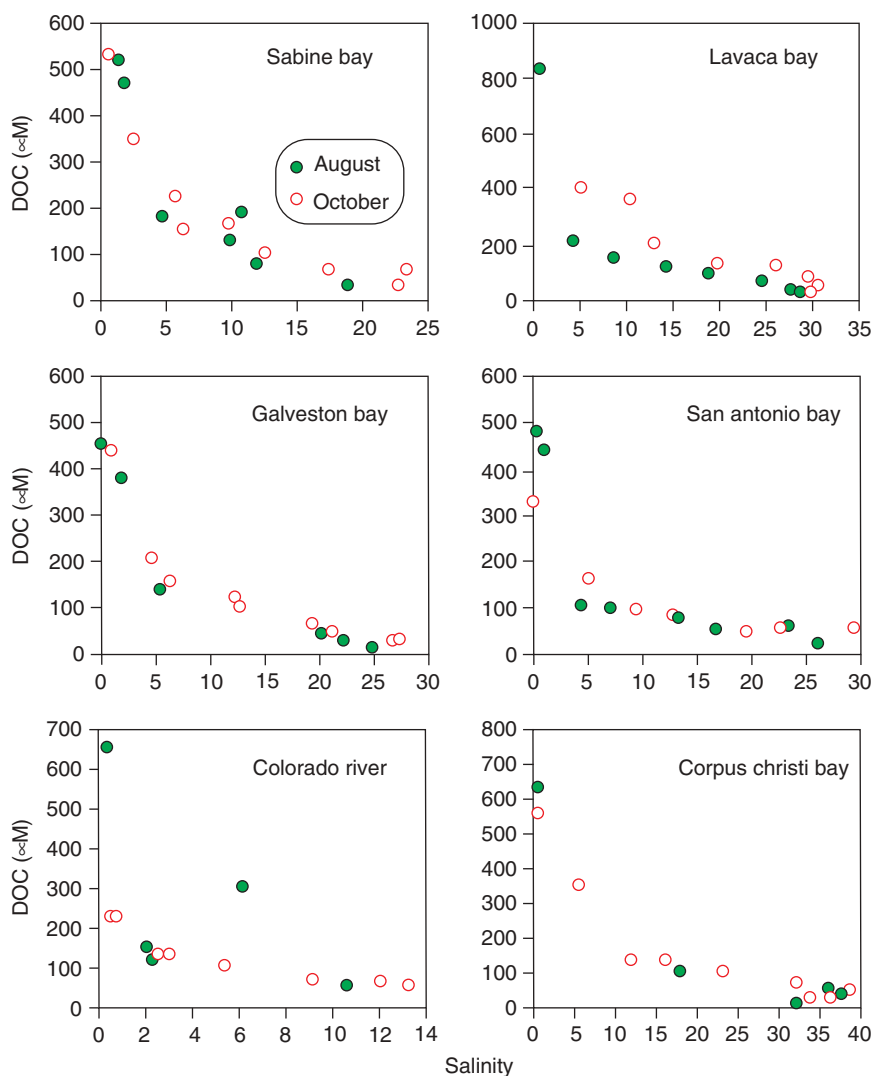
Salinity gradients of DOC concentrations have commonly been used to examine conservative and nonconservative behavior of DOC in estuaries (Guo
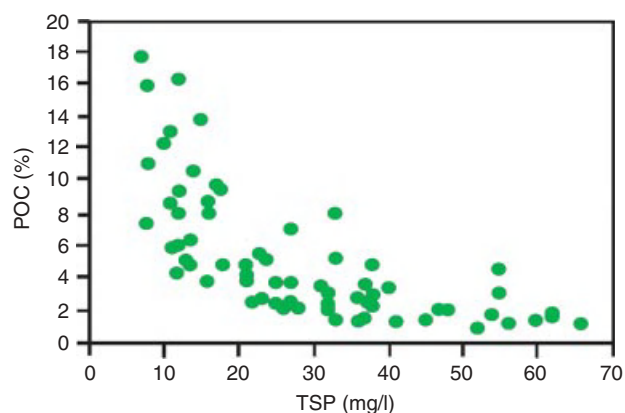
FIGURE 3.18 Percent particulate organic carbon (POC) and total suspended particulates (TSP) in the water column from three regions of the Sabine–Neches estuary, sampled from March 1992 to October 1993. *Source:* Modified from Bianchi et al. (1997).

et al., 1999, and references therein). The typical DOC mixing gradients for six different estuaries in the Gulf of Mexico clearly indicated that decreases in DOC concentration with increasing salinity are occurring nonconservatively (Fig. 3.19; Benoit et al., 1994). The concentrations of DOC at the lower salinity regions are due to riverine inputs of DOC. Seasonal variability of phytoplankton blooms can change the distribution of DOC in estuaries, whereby higher concentrations of DOC co-occur with the blooms in the lower estuarine region because of lower light attenuation rates. The lower salinity regions appear to be important sinks for DOC; this is within the region of the ETM where fractions of DOC can be removed by coagulation, flocculation, and other processes.

Other important subcomponents of the total DOC pool are the high- and low-molecular-weight dissolved organic carbon (HMW DOC and LMW DOC); the HMW DOC is sometimes referred to as *colloidal organic carbon*. If, for the moment, any effects that different techniques and filters may have on collecting the amounts and composition of HMW DOC are excluded, it is seen that there are significant differences in the relative importance of HMW DOC in estuaries. Sources of HMW DOC could be derived from old soil materials, fresh litter from terrestrial runoff, or perhaps more labile algal sources (both benthic and pelagic) in the estuary. Radiocarbon values of two size fractions of HMW DOC reveal that the smaller size fraction (>1 kDa) was younger than the larger (>10 kDa), with both being higher in abundance in

FIGURE 3.19 Concentrations of dissolved organic carbon (DOC) across a salinity gradient in six Texas estuaries in August and October. *Source:* Modified from Benoit et al. (1994).

the lower salinity region of Galveston Bay estuary (USA; Guo and Santschi, 1997). These differences were attributed to inputs of older HMW DOC (more geopolymerized) from porewaters in resuspended sediments. The importance of older HMW DOC from porewaters to estuarine waters has also been shown to be important in coastal bottom waters along shelf regions in the Mid Atlantic Bight (Mitra et al., 2000).

This does not support the open ocean size-reactivity model proposed by Amon and Benner (1996), which, simply stated, predicts that the "older" fraction of DOC will reside in the lower molecular weight classes, typically at deeper water depths. However, the size-reactivity model is generally observed in oceanic waters because of the selective removal of labile "younger" C as POC produced in the euphotic zone sinks through the water column, accumulating the "older" smaller molecular weight DOC at depth (Amon and Benner, 1996; Guo et al., 1996).

Bulk radiocarbon and ^{13}C signatures of both total POC and DOC pools have also proven useful in constraining what their sources might be in estuaries (McCallister et al., 2004, and references therein). For example, $\Delta^{14}C$-DOC is always more ^{14}C enriched compared with $\Delta^{14}C$-DOC along riverine margins of the US East Coast estuaries (Raymond and Bauer, 2001a). Since the ^{14}C-enriched DOC is also more depleted in ^{13}C, it appears that these differences are due to greater contribution of ^{14}C-enriched soil and litter-fall organic matter that is leached from soils. Similarly, recent work has shown, using a dual-isotopic tracer approach of isotopic signatures ($\delta^{13}C$ and $\Delta^{14}C$) for bacterial nucleic acids collected from different regions and potential C source materials, that there was good delineation of C sources from aquatic and terrestrial systems in the York River estuary (McCallister et al., 2004). In general,

the results from these dual-isotopic tracer studies indicate that the broad classification of organic C, and the interchangeable use of the terms *old* and *refractory*, is in many cases not valid. In fact, highly depleted ^{14}C (1000–5000 years old) in the Hudson River estuary appears to be an important labile source fueling heterotrophy (Cole and Caraco, 2001). Thus, the storage of organic matter for centuries and millennia in soils and rocks can actually become available to aquatic microbes over periods of weeks to months (Petsch et al., 2001), completing a unique linkage between river metabolism and the history of organic matter preservation in the drainage basin (Cole and Caraco, 2001).

In estuarine sediments, down-core concentrations of bulk C indices, such as total organic C (TOC), $\delta^{13}C$, and C:N ratios can be used as a general index of the loading and sources of POC to sediments. There are a number of problems with using the C:N ratio as the only diagnostic indicator of organic matter source; however, if coupled with stable isotope and chemical biomarker tools, sources are better constrained. If bulk C tools are simply used to examine down-core sediment profiles, TOC and atomic C:N ratios in sediments from the York River estuary (USA) clearly reflect a dominance of phytoplankton inputs, with a typical % TOC in surface sediments of estuaries, decreasing with diagenetic "burn-off" at depth (Arzayus and Canuel, 2004). The bulk $\delta^{13}C$ signal also reflects inputs of phytoplankton sources. Down-core profiles of porewater bulk DOC and C:N ratios (of DOM) should also reflect changes in rates of POM remineralization. This is illustrated in down-core profiles of DOC, C:N ratios, and ΣCO_2 at three stations in Chesapeake Bay (Fig. 3.20; Burdige and Zheng, 1998).

Differences in these DOC profiles are controlled primarily by differences in the physical and biogeochemical processes in sediments in the upper, middle,
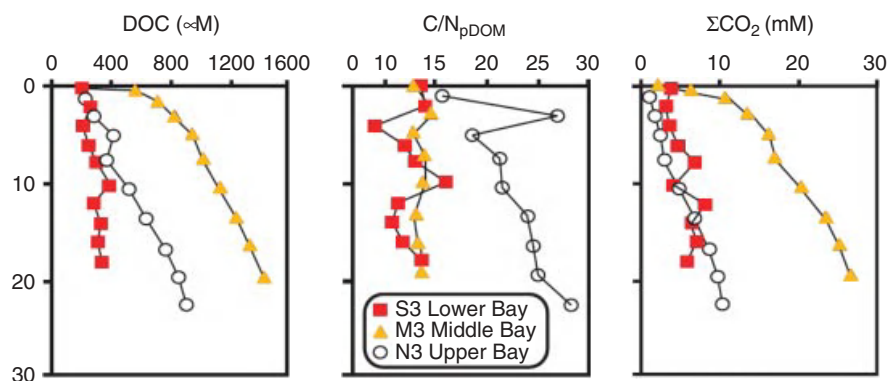
FIGURE 3.20 Down-core profiles of porewater dissolved organic carbon (DOC), C:N ratios, and total ΣCO_2 at three stations in Chesapeake Bay. *Source:* Modified from Burdige and Zheng (1998).

and lower regions of the bay. More specifically, the higher porewater DOC concentrations at the mid-Bay station are due to higher remineralization and a greater storage of the remineralization "signature" (e.g., DOC and ΣCO_2), due to lower O_2 conditions and less physical mixing than at stations in the upper and lower regions of the bay. Changes in the C:N ratios of porewater DOM at these stations are likely due to differences in the selective utilization of N-rich DOM, and not due to differences in source inputs (e.g., terrestrial vs marine), as originally thought (Burdige, 2001). Thus, redox (more consistently anoxic vs "mixed" redox) and the presence/absence of macrofauna were the most important controlling factors in determining the remineralization of POM to DOM and overall storage of DOM in Chesapeake Bay sediments.

3.6 CONCLUDING REMARKS

A major recent realization by earth, aquatic, and marine scientists is that virtually all systems have been already altered by both direct and indirect aspects of human activity and alteration. That is, our findings of the ecological and biogeochemical function of these systems are increasingly biased away from natural to altered states. Human activities can have a variety of effects on watersheds, rivers, and estuaries, sometimes in opposite senses. Deforestation, tillage, hydrological alteration, and irrigation-enhanced erosion have increased loads of sediments and particulate carbon to rivers. Widespread construction of dams, however, has resulted in significant retention of carbon and sediments in reservoirs (see reviews by Bauer and Bianchi, ; Bianchi and Bauer,). Furthermore, the reduction of river-suspended loads by dams around the world has generally resulted in increasing light availability and the potential role of phytoplankton biomass in river and estuarine biogeochemistry. To better understand the anthropogenic effects, long-term monitoring studies on rivers and estuaries will continue to be valuable tools for assessing change due to both natural and human factors.

Estuaries are tremendously sensitive to long-term global climate change. Changes in river discharge in a warming climate are predicted to be particularly large in Arctic regions as snow pack and glacial water retention decreases and precipitation and runoff increase. Rising sea levels that outpace the growth of estuary mouth sills (or bars) could also subject previously protected estuaries to increased wave energy regimes, altering the depositional and redox environment on estuary floors. Dramatic fluctuations in major biogenic nutrient (N, P, and Si) loading alone over the past 50–75 years have undoubtedly led to fluctuations in C and organic matter fluxes and cycling in rivers and estuaries, which may be unprecedented over at least the Holocene, if not longer. Nonetheless, it is imperative that monitoring studies of rivers and estuaries, not only to document changing hydrological conditions but also to assess changes in soil organic matter losses and concomitant changes in river and estuarine carbon and organic matter inputs are critical for providing baseline information for future studies and assessments of the impacts of these changes in river, estuarine, and coastal ocean biogeochemical cycles, metabolic balances, and ecosystem function.

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# CHAPTER **FOUR**

ESTUARINE PHYTOPLANKTON

Hans W. Paerl and Dubravko Justić

4.1 INTRODUCTION

Phytoplankton means ''drifting plant'' in Greek. These planktonic microalgae comprise several taxonomic groups (e.g., chlorophytes, chrysophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates; Fig. 4.1) that conduct a large share of photosynthesis and primary production and play a central role in carbon, nutrient (i.e., N and P), and oxygen cycling in estuarine and coastal waters (jointly termed *coastal waters*). In most coastal ecosystems, phytoplankton account for at least half of ecosystem primary production (Cloern, 2001; Harding et al., 2002). Hence, phytoplankton are of fundamental importance in supporting estuarine food webs. They are also key drivers of biogeochemical cycling and play a central role in determining water quality. Phytoplankton have fast growth rates, in the order of one doubling per day, and members of some groups (dinoflagellates, cryptophytes, and cyanobacteria) can proliferate in explosive ways, forming dense ''blooms'' that can discolor affected waters and cause water quality problems (Paerl, 1988; Hallegraeff, 1993; Richardson, 1997; Anderson et al., 1998). When blooms die or ''crash,'' they can sink to the seafloor, where they decompose rapidly and fuel high rates of oxygen consumption, leading to oxygen-depleted bottom waters (i.e., hypoxia and anoxia; Officer et al., 1984; Rabalais and Turner, 2001; Diaz and Rosenberg, 2008). Some bloom species also produce foul odors and tastes, which can be problematic from water supply, recreational,

and aquaculture perspectives. Lastly, some species produce secondary metabolites that can be toxic to higher fauna (Carmichael, 2001), including zooplankton grazers, fish, and a variety of mammals, including humans.

A bulk of the phytoplankton exists as microscopic solitary cells, although some form multicellular chains and others form aggregates that are visible to the naked eye. They exist in several size classes, including the picoplankton (<2 μm), nanoplankton ($2-20$ μm), and microplankton (>20 μm). The relative contributions of these size classes to total phytoplankton biomass vary according to nutrient status, physical (temperature, irradiance, and mixing), and hydrologic (freshwater discharge) conditions, as well as climatic regimes. Generally, phytoplankton cells are denser than water, having silica, cellulose, and/or carbonate components, and thus tend to sink. Various mechanisms allow phytoplankton to remain in the illuminated upper water column. Some cells remain easily suspended because of their diminutive size. Others glide or actively swim (i.e., flagella), while some adjust their buoyancy by altering cellular density, or forming cellular vesicles that contain gases or oils. Major phytoplankton groups (e.g., diatoms, dinoflagellates, and cyanobacteria) form cysts and inactive cells as ''resting stages'' during unfavorable growth periods that sink to the sediments. These cells may be reactivated when favorable conditions reappear (Smetacek, 1985).
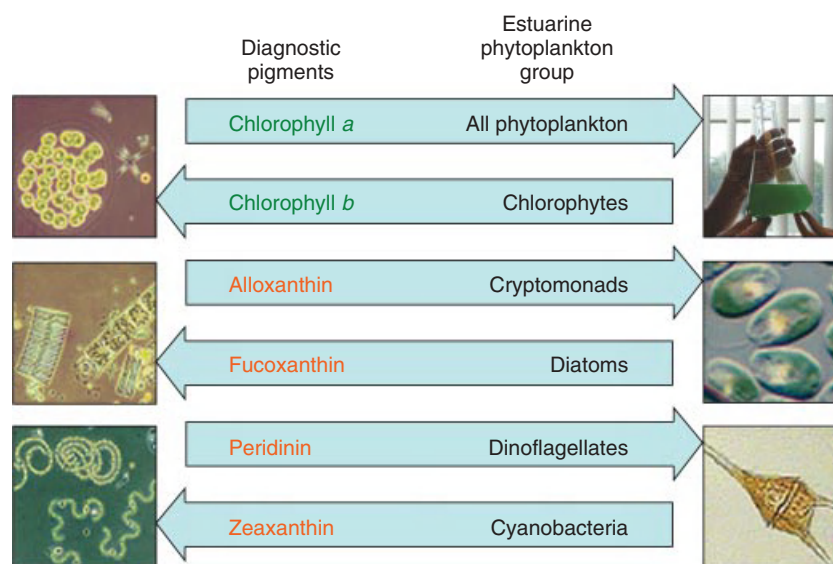
FIGURE 4.1 Examples of the major estuarine phytoplankton groups and their diagnostic photopigments. *Source:* From Paerl et al., 2005.

4.2 THE PLAYERS: PHYTOPLANKTON COMMUNITY COMPOSITION AND FUNCTION

Coastal phytoplankton communities can be grouped taxonomically and functionally; each approach has specific relevance and application with regard to trophic and biogeochemical roles that these groups play. Taxonomically, the phytoplankton can be divided into prokaryotic and eukaryotic groups.

4.2.1 Cyanobacteria

Cyanobacteria are prokaryotic phytoplankton that have bacteria-like cellular features (i.e., lack of well-defined nucleus and no membrane bound organelles). The cyanobacteria exist in spheroid single or aggregated cells, aggregated or solitary nonheterocystous filamentous, and heterocystous filamentous groups (Stanier and Cohen-Bazire, 1977; Komarék and Anagnostidis, 1986). Heterocysts are thick-walled cells that house oxygen-sensitive nitrogen (N_2) fixation (Wolk, 1982), an important physiological process. This enables these taxa to simultaneously photosynthesize and fix atmospheric N_2, converting it to biologically available ammonia (NH_3; Fogg, 1982; Paerl and Zehr, 2000). Nitrogen fixation provides biologically available N during N-limited conditions, which frequently characterize coastal waters. Some spheroid and nonheterocystous filamentous groups can also fix N_2, mostly during darkness and in oxygen-deplete microenvironments (aggregates, biofilms, mats, and as endosymbionts). This can restrict their distributions (Paerl and Zehr, 2000; Paerl and Kuparinen, 2002; Zehr and Paerl, 2009).

Interestingly, while N_2 fixing cyanobacteria are capable of meeting their N requirements under N-depleted conditions, these diazotrophs (i.e., N-fixing taxa) rarely dominate the phytoplankton communities in N-depleted estuaries. Notable exceptions are brackish, lagoonal, and periodically stratified waters, where water column stability and low salinity appear to favor this group (Paerl, 1990; Paerl and Zehr, 2000). In the brackish Baltic Sea, extensive blooms of heterocystous filamentous genera (*Aphanizomenon*, *Anabaena*, and *Nodularia*) occur during vertically stratified summer months (Kononen et al., 1996). These blooms are significant sources of ''new'' N supporting production and eutrophication of the Baltic Sea (Elmgren and Larsson, 2001). Other examples include non- or microtidal lagoonal estuarine systems such as Peel-Harvey Estuary in Australia (*Nodularia*; Huber, 1986), Lake Ponchartrain, LA (*Anabaena*; Dortch et al., 1999), and the subestuaries (Chowan, Neuse) of the lagoonal Pamlico Sound system, NC (Paerl et al., 1983, 2001). Salinity does not appear to be a barrier to the expansion of diazotrophic cyanobacteria in estuaries (Moisander and Paerl, 2000; Moisander et al., 2002a). Grazing pressure, likewise, does not explain the puzzling lack of diazotrophic cyanobacterial dominance (Paerl et al., 2001). However, physical

constraints, including excessive turbulence, persistent vertical mixing, and high rates of flushing (i.e., short residence time) that characterize many of the world's estuarine and coastal ecosystems, prevent dominance by these otherwise opportunistic genera (Paerl and Zehr, 2000; Moisander et al., 2002b). This may help explain why chronic N limitation persists in these systems, (i.e., biological N_2 fixation cannot meet ecosystem N demands).

Blooms of the heterocystous N_2 fixing cyanobacteria can produce a variety of odor and taste compounds (geosmins and 2-methylisoborneol), rendering affected waters unsuitable for consumption, aquaculture, and recreational purposes (Stewart and Falconer, 2008). Lastly, some cyanobacterial bloom species produce alkaloid, peptide, and other compounds that can be toxic on ingestion or contact with affected waters (Carmichael, 1997, 2001; Stewart and Falconer, 2008).

The subtropical-tropical oceanic, nonheterocystous, filamentous N_2 fixing genus *Trichodesmium* can, at times, make excursions into coastal waters when it is carried in major currents (Atlantic and Gulf of Mexico Gulf Stream, Kuroshio current in the South China Sea) that take it close to coastal regions. *Trichodesmium* blooms can be spectacular when concentrated in these current systems, forming yellow-brown slicks of aggregated filaments, referred to as *sea sawdust* (Fogg, 1982; Paerl, 1999). *Trichodesmium* blooms can provide a major source of ''new'' N supporting primary production in these waters (Capone et al., 1997). They also produce secondary metabolites that may play a role in deterring grazing by dominant crustacean zooplankton (Hawser et al., 1992), and thereby affect food web dynamics.

The remaining non-N_2 fixing cyanobacterial genera make up an important, and at times dominant, fraction of estuarine phytoplankton biomass. In particular, small (<3 μm) coccoid ''picoplanktonic'' cyanobacteria (*Synechococcus* spp. and *Prochlorococcus* spp.) can at times constitute more than 50% of estuarine phytoplankton (Marshall and Lacoutre, 1986; Ray et al., 1989; Gaulke et al., 2010).

The eukaryotic coastal phytoplankton are partitioned into the following major groups: the chlorophytes—or green algae, the cryptophytes—dominated by cryptomonads, the chrysophytes—dominated by numerous flagellates, the bacillariophytes—or diatoms, the prymnesiophytes, and the dinophytes—or dinoflagellates. Each group plays an important role in primary production, food web dynamics, and biogeochemical cycling. They also differentially (and at times uniquely) respond to nutrient enrichment, hydrologic forcing (freshwater discharge and salinity regimes), irradiance gradients, and grazing pressures.

4.2.2 Chlorophytes

Chlorophytes or ''green algae'' are common and at times dominant in the low salinity, upstream segments of estuaries (Tomas, 1997). They exist as free-floating solitary or aggregated cells varying in size and shape, from small coccoid cells (2- to 5-μm diameter) resembling the picoplankton to larger ovoid- and disk-shaped cells (the desmids) that can exists as small groups of stacked cells (e.g., *Scenedesmus*). The chlorophytes also contain flagellated genera (e.g., *Chlamydomonas*) that can accumulate as bright-green blooms. Chlorophytes have relatively fast growth rates and thrive in well-flushed, short residence time, low salinity waters. These waters tend to have elevated nutrient concentrations, favoring fast-growing species. While the chlorophytes can form blooms, there are no known toxic species and hence blooms are not considered to be particularly ''harmful.'' Large accumulations of ungrazed cells can, however, contribute to bottom water hypoxia by sinking out of the illuminated euphotic zone.

4.2.3 Cryptophytes

Cryptophytes, while taxonomically distinct from the chlorophytes, have similar morphological and ecological characteristics. Cryptophytes are similar in size to the chlorophytes and possess flagella, which help them maintain an optimal position, relative to light and nutrient conditions, in the upper water column (cf., Tomas, 1997; Reynolds, 2006). Almost all cryptophytes are unicellular and ovoid in shape (e.g., the genus *Cryptomonas*). They are asymmetric, with two unequal flagella located on one end of the cell. These serve as forward and reverse ''thrusters,'' propelling them in a distinct (from chlorophytes) and highly effective manner. Most cryptophytes also have an ''oral groove,'' which helps them capture small prey items, such as bacteria. This provides considerable metabolic flexibility, enabling the cells to function in photosynthetic autotrophic and heterotrophic modes. Some cryptophytes have ''lost'' their photosynthetic apparatus (e.g., *Goniomonas* spp.); hence, they derive all their nutrition heterotrophically. The photosynthetic cryptophytes contain chlorophylls *a* and c_2, xanthophylls, and an either blue or red phycobiliprotein. This imparts a brownish, reddish, or even bluish color to blooms. Their preferred habitat is fresh to brackish nutrient-enriched waters. As a result, blooms are often observed just upstream of strong salinity gradients, in the oligohaline regions of estuaries.

Blooms are not known to be toxic. The most ''harmful'' aspect of these blooms is that they can contribute significant amounts of organic matter to bottom waters when they die, potentially enhancing hypoxic conditions.

4.2.4 Chrysophytes

Chrysophytes contain chlorophyll *a* and a yellowish-brown carotenoid pigment called *fucoxanthin*. Blooms typically appear light brown to golden in appearance. Most species are free-swimming (flagellar) and unicellular, but some exist as colonial forms. Chrysophytes have complex life cycles and some may spend part of their life as amoeboid cells. They also have quite complex morphologies. For example, the freshwater genus *Dinobryon* has individual cells that are surrounded by vase-shaped loricae, composed of chitin fibrils and other polysaccharides. The colonies grow as branched or unbranched chains. A colonial form, *Synura*, has cells that are covered by silica scales. Some species are colorless, but most contain photosynthetic pigments. They exhibit a great deal of metabolic flexibility; for example, they can be facultative heterotrophs in the absence of light or when high concentrations of dissolved organic matter are present.

In recent years, the toxic picoplanktonic chrysophyte *Aureococcus anophagefferens* and related species have proliferated as ''brown tides'' in estuaries along the US Northeast and mid-Atlantic as well as some of the Texas Gulf of Mexico lagoonal estuaries (Bricelj and Lonsdale, 1997; Gobler et al., 2002). This motile species has bloomed at densities high enough to effectively ''shade out'' bottom-dwelling higher plant (seagrass) and benthic microalgal communities, leading to increases in hypoxic conditions, and adversely affecting bottom habitat for infauna, including commercially important shellfish species. The recent upsurge of this chrysophyte appears linked to a complex set of biogeochemical changes brought about by droughts, excessive groundwater withdrawal, and nutrient enrichment in nearby coastal regions, which have locally increased salinity, nutrient, and organic matter concentrations. In addition, increased hypoxia and other adverse effects on the infauna in these habitats have reduced grazing on this organism, further increasing its dominance (i.e., positive feedback; Gobler et al., 2002).

4.2.5 Diatoms

Diatoms belong to the class Bacilariophyceae of the phylum Bacilariophyta. They are among the most abundant, widespread, and productive phytoplankton in coastal waters and serve a central role in planktonic food webs (Hasle et al., 1996). Diatoms tend to prefer waters with moderate to high nutrient concentrations. They are capable of very fast growth rates, on the order of two doublings per day or even faster, and as such tend to bloom during springtime, when relatively high nutrient loads often coincide with maximum freshwater runoff conditions or when upwelling might take place. In general, diatoms are an excellent source of food for grazers, including zooplankton, benthic filter feeders, larvae, and planktivorous fish (e.g., menhaden). Several diatom genera (*Rhizosolenia* and *Hemiaulus*) have species capable of hosting endosymbiotic N_2 fixing cyanobacteria, which facilitate growth under N-limited conditions.

Morphologically, diatoms are complex, as their siliceous cell walls or frustules take on many different shapes and sizes. There are two major groups, defined by the general shapes of the frustules, the boat-shaped pennates and round, pill-box-shaped centrates. Pennate diatoms are generally indicative of benthic forms, but they are often resuspended from the bottom to become important in plankton communities. Diatoms occur as either solitary or joined (in chains) planktonic cells or attached to a substratum by means of gelatinous extrusions or long chains. Some species are capable of movement via ''jet propulsion'' accomplished through mucilaginous excretions, while other species are free floating and are dependent on currents for transport. Diatoms have complex life cycles that involve benthic ''resting stages'' that tend to occur after an extended pelagic growth phase (Smetacek, 1985). Diatom cells range in size from 2 μm to well over 100 μm. Because they rely on silicon for cell wall formation, growth, and reproduction of diatoms may, at times, be controlled or ''limited'' by silicon supply. Silicon limitation can be particularly evident when nitrogen and phosphorus supplies are elevated relative to silicon as a result of ''cultural eutrophication'' (Officer and Ryther, 1980; Turner et al., 1998; Humborg et al., 2008).

Diatoms are considered highly desirable phytoplankton in estuaries, in that they support key planktonic and benthic food webs (Hasle et al., 1996; Tomas, 1997; Reynolds, 2006). However, some species produce toxins that may be harmful to resident grazers and higher level consumers, including man. One toxic genus, *Pseudonitzchia*, can be problematic, and it appears to have increased in bloom frequency in response to eutrophication in the Mississippi discharge plume of the northern Gulf of Mexico and other estuaries (Parsons et al., 2002). The causes of *Pseudonitzchia* blooms are unclear but may be related

to overall increases in nutrient loading and shifts in ratios of nutrient supply (Parsons et al., 2002).

4.2.6 Prymnesiophytes

Prymnesiophytes, or *haptophytes*, include about 500 species in 50 genera, with many additional fossil genera and species, most notably the coccolithophorids. This group is primarily unicellular, photosynthetic, and constitutes an important source of food in coastal waters (Tomas, 1997). Prymnesiophytes, while containing chlorophyll, are often a golden-brown color because of the presence of the carotenoid accessory pigments diadinoxanthin and fucoxanthin. Prymnesiophytes may have a complex life cycle, altering between motile and nonmotile morphologies. Many prymnesiophytes are covered with scales, which, such as diatoms, can lead to complex architecture. They also have spines and various species have quite diverse morphologies. They may be calcified (calcium carbonate) and rarely comprise silica plates.

Prymnesiophytes of the genus *Chrysochromulina* form blooms that can cause serious fisheries problems. Large blooms, such as those that have been reported in the Baltic Sea region are problematic because of the mucilage surrounding the algal cells, which may clog fish gills and also render them permeable to dissolved toxins (cf., Richardson, 1997). Another problem with blooms is the production of dimethyl sulfide, a noxious-smelling compound that can alter fish migration routes, adversely affecting the ecology and sustainability of commercial and recreational fish species.

4.2.7 Dinoflagellates

Dinoflagellates are unicellular, highly evolved phytoplankters that are morphologically and functionally diverse. Their cell sizes range from less than 10 μm to over 1000 μm (Hasle et al., 1996; Reynolds, 2006). Dinoflagellate means "whirling flagella." Each dinoflagellate has two flagella, facilitating rapid forward and lateral movement. Dinoflagellates are surrounded by a complex covering called the *amphiesma*, which consists of outer and inner continuous membranes, and between which lie a series of flattened vesicles. In armored forms, these vesicles contain cellulose plates called *thecae*. If this armor is lacking or shed under certain environmental conditions, the cells are "naked."

Most dinoflagellates are photosynthetic, possessing chlorophyll *a* and accessory pigments, including the diagnostic carotenoid peridinin. Dinoflagellates are important and at times dominant estuarine primary producers, sustaining the grazing component

of the food web. Some dinoflagellates are facultative heterotrophs, engulfing and ingesting bacteria and smaller phytoplankton as prey and also consuming dissolved organic carbon compounds. Even though their growth rates are generally slower than chlorophytes, cryptophytes, and diatoms, dinoflagellates can form large, and in some cases harmful, blooms in estuaries. Examples include several red tide species (e.g., *Karenia brevis* and *Noctiluca* spp.) that are toxic to a wide variety of finfish, shellfish, and other fauna, including humans. These organisms are often of oceanic origins but can enter and proliferate in estuaries, especially during summer months (Hasle et al., 1996). These dinoflagellates produce neurotoxins that affect muscle function in susceptible organisms. Humans may also be affected by eating fish or shellfish containing the toxins. The resulting diseases include ciguatera (from eating affected fish) and paralytic shellfish poisoning (from eating affected shellfish, such as clams, mussels, and oysters); they can be serious but are not usually fatal. Other more exclusively estuarine toxic dinflagellates include *Karlodinium, Gymnodinium*, and *Prorocentrum* species (Hasle et al., 1996). These species produce toxic substances that have been implicated in fish kills. Their increased presence and proliferation has been linked to eutrophication. Other nontoxic dinoflagellate blooms are linked to seasonal patterns of freshwater runoff, salinity, and light regimes. These blooms are often composed of highly desirable nontoxic genera (e.g., *Heterocapsa*) that are of central importance in supporting estuarine food webs. One of the more interesting biological properties of dinoflagellates is the ability of some species to produce light through bioluminescence, the same mechanism that makes fireflies glow. In addition, there are some dinoflagellates that are parasites on fish or on other protists (Hasle et al., 1996).

4.2.8 Phytoplankton Communities

Phytoplankton communities are dynamic multispecies assemblages that exhibit spatial patchiness (microns to meters) and temporal variability over scales ranging from minutes to days (Dustan and Pinckney, 1989). Because these primary producers play a central role in the regulation of estuarine biogeochemical cycling, detailed characterizations of the community-level processes that structure phytoplankton communities are essential for understanding overall ecosystem dynamics. A critical prerequisite for characterizing these processes is the ability to determine the taxonomic composition of natural phytoplankton assemblages reliably and accurately.

The high degree of inherent spatiotemporal variability at the ecosystem scale requires that analytical approaches for describing phytoplankton taxonomic diversity be applicable for processing large numbers of samples quickly with minimal cost. The most reliable technique for enumerating single species in mixed phytoplankton samples is microscopic counts, but these are tedious, require a high level of expertise, and are costly. In addition, species-level identification and enumeration may not be necessary for examining larger scale phytoplankton impacts on biogeochemical cycling and trophodynamics. Often, examinations at courser taxonomic levels (i.e., class and group) are effective and make quantification easier. Chemosystematic pigments encoding specific functional phytoplankton groups (i.e., diatoms, chlorophytes, dinoflagellates, cyanobacteria, and cryptomonads, Fig. 4.1) can also be used (Jeffrey et al., 1997, 1999). In particular, carotenoids specific for different algal groups provide diagnostic biomarkers for determining the relative abundance of key phytoplankton groups. Photopigment extracts from natural microalgal samples can be separated and quantified by high performance liquid chromatography (Millie et al., 1993; Wright et al., 1996; Paerl et al., 2003). Photopigments that have been used as markers are shown in Figure 4.1 and detailed in the study by Paerl et al. (2003). When compared to total phytoplankton biomass (based on chlorophyll *a*) and cell counts, diagnostic photopigments can quantitatively determine the contributions of each phytoplankton group (Tester et al., 1995; Lewitus et al., 2005).

Molecular techniques that are useful for assessing phytoplankton diversity are rooted in organic chemistry and fundamentally rely on obtaining an informative molecule (e.g., nucleic acid) from phytoplankton cells. The following paragraphs outline some of these molecular techniques. References are provided for students who want to acquire more information on this subject. DNA is a commonly targeted molecule used in diversity studies, although RNA may also be used. Both nucleic acid forms are informative molecules because they contain a ''code'' or series of nucleotides. Stretches of nucleotides can be specifically amplified (using primers and the Polymenrase Chain Reaction, PCR), cloned, sequenced, and then these sequences can be compared by various phylogenetic analyses (e.g., phylogenetic tree building). Diversity estimates can be done based on the number of individual sequences obtained per cloning effort (rarefaction curves).

Commonly, rRNA genes are targeted and sequenced to study genus-level phytoplankton diversity. This is primarily due to the vast number of publically available rRNA sequences obtained to originally study the evolution of life (Woese and Fox, 1977; Pace et al., 1985). Because of the conserved nature of rRNA genes, the phylogenetic resolution (i.e., ability to distinguish phytoplankton) is limited to around the genus level. Other genomic regions that evolve more rapidly than rRNA genes, such as the ITS region, the rRNA intergenic spacer region, or other intergenic regions (Urbach et al., 1998; Rocap et al., 2002) can better differentiate populations to a subgenus level. Also, protein encoding genes have been targeted for diversity studies that are focused on the diversity of organisms capable of a particular metabolic activity such as nifH encoding for the nitrogenase enzyme or rbcL encoding for RuBisCO subunit (John et al., 2006; Zehr and Paerl, 2009). With a sequence database in hand, fingerprinting techniques (e.g., Terminal Restriction Fragment Length Polymorphism, TRFLP, Automated rRNA Intergenic Spacer Analysis, ARISA, or Denaturing Gradient Gel Electrophoresis, DGGE; e.g., Diez et al., 2001) can be used to distinguish differences in phytoplankton communities between samples.

RNA is also a useful and targetable molecule for studying phytoplankton diversity. Largely due to the susceptibility of RNA to enzyme degradation, its use first requires reverse transcription to cDNA. Recently, applied approaches utilize an amplification step before cDNA synthesis, so that small quantities of RNA that can be quickly and efficiently sampled can still be used for sequence analysis (Frias-Lopez et al., 2008). Examining the sequence diversity of RNA provides an indication of phytoplankton that are presumably active in the environment (where as DNA is indicative of presence or absence). For example, rbcL transcripts recovered off the coast of FL were indicative of shifts in the major phytoplankton in the Mississippi River plume region (Paul et al., 2000).

With a core sequence library, several approaches can then be taken to examine diversity further. For example, quantitative PCR (qPCR) may be used to enumerate portions of phytoplankton diversity across samples. More and more researchers are turning to high throughput methods to obtain sequence data. Recent approaches have aimed to bypass the necessity of PCR amplification (which may have influential biases) for diversity studies by collecting large amounts of biomass from the environment and directly sequencing molecules from this biomass. Despite impressive bioinformatic and high yield sequencing advances, the diversity of phytoplankton (and heterotrophic plankton) in the environment is still too high for random sampling to be useful for assessing diversity (Venter et al., 2004).

Targeted high throughput sequencing in this manner (e.g., targeting variable regions of the 16S rRNA gene) appears to carry some value for assessing diversity (Huse et al., 2008).

4.3 SPATIAL AND TEMPORAL PATTERNS OF PHYTOPLANKTON BIOMASS AND PRODUCTIVITY

Phytoplankton often account for at least half of ecosystem primary production in coastal waters. Their rates of primary production are remarkably variable and range from near undetectable to several $gC/m^2/day$. Phytoplankton also have fast growth rates. Hence, they can rapidly respond to diverse chemical (nutrients and toxicants), physical (light, temperature, and turbulence), and biotic (grazing) impacts over a wide range of concentrations and intensities. Changes in phytoplankton communities often precede changes in ecosystem function, including shifts in material flux, oxygen balance, food webs and fisheries, and potentially, permanent losses of higher plant and animal assemblages.

Coastal phytoplankton communities typically show strong seasonal and spatial distributions. This is illustrated for Pamlico Sound and Chesapeake Bay, two of the largest estuarine systems in the United States (Figs 4.2 and 4.3). In both systems, the distribution of phytoplankton biomass, as chlorophyll *a*, is strongly influenced by the delivery of freshwater (i.e., discharge), which also delivers watershed-based nutrients to support new primary productivity and the development of phytoplankton biomass. In addition to being a source of new nutrients, freshwater discharge also determines flow rates, flushing, and resultant residence time of estuarine waters, that is, the amount of time it takes for fresh water and nutrients delivered to the estuary to move through the system before exiting to the coastal ocean. Flushing rates and residence times are strong determinants of where the maximum amount of phytoplankton biomass can develop and build up in response to nutrient inputs. For example, during high flow periods, nutrient delivery to the system will be high. Simultaneously, high flow will create short residence time conditions, restricting phytoplankton growth and biomass buildup to the most downstream, widest and longest residence time segments of the estuary, a phenomenon that is illustrated in Figures 4.2 and 4.3. In the Pamlico Sound system, high flow conditions typically lead to maximum phytoplankton biomass (as Chl *a*) in the downstream

segments of the estuaries and open waters of the Sound itself (Fig. 4.2), while under low flow, long residence time conditions, phytoplankton biomass maxima are typically in the upper estuarine regions.

Most phytoplankton are phototrophs; hence, photosynthetic activities and growth rates are strongly controlled by the availability and quality of light (Cloern, 1999; Reynolds, 2006). Photosynthetic as well as carbon and nutrient assimilatory processes, respiration, energy metabolism, and growth are mediated by enzymes that are temperature sensitive. As such, seasonality plays an important role in the control of photosynthetic production (primary production), biomass, and composition (cf., Harrison and Turpin, 1982; Marshall and Lacoutre, 1986; Malone et al., 1996; Pinckney et al., 1999; Valdes-Weaver et al., 2006). Typically, maximum rates of primary production and growth occur during springtime when light and/or nutrient availability are both high, leading to spring bloom conditions. If nutrient availability remains high during summertime through input and/or recycling, blooms may persist throughout this period. These are also periods of maximum temperatures, favoring relatively high growth rates. Not all phytoplankton groups and individual species respond similarly to shifting light, temperature, and nutrient gradients; this is largely due to the individual energetic, nutrient, and other requirements (e.g., water column stability, salinity, trace metals, pH, and dissolved inorganic carbon) for supporting and sustaining optimal growth. Differential grazing on these groups and species may exert selective ''top-down'' control.

Some dinoflagellate species show sudden, strong positive responses to increases in light levels and day length that occur in late winter. This, combined with increased nutrient-enriched runoff and a lack of intense grazing create ideal conditions for large blooms (e.g., *Heterocapsa* spp.) that can occur as early as late January in temperate waters (Paerl et al., 1998; Litaker et al., 2002).

Other phytoplankton groups dominate during spring and summer. Typically, diatoms tend to bloom in early spring, because they exhibit relatively fast growth rates, even at fairly low temperatures and hence can take advantage of early spring freshwater runoff (Harding, 1994; Harding et al., 2002; Valdes-Weaver et al., 2006; Harding and Miller, 2009). If runoff is extremely high such as during spring floods, large segments of estuaries can turn fresh; these conditions typically favor chlorophytes and a variety of flagellates (cryptomonads and chrysophytes), which prefer low salinity, high nutrient supply conditions (Paerl et al., 2006a,b; Valdes-Weaver et al., 2006). Motile taxa such
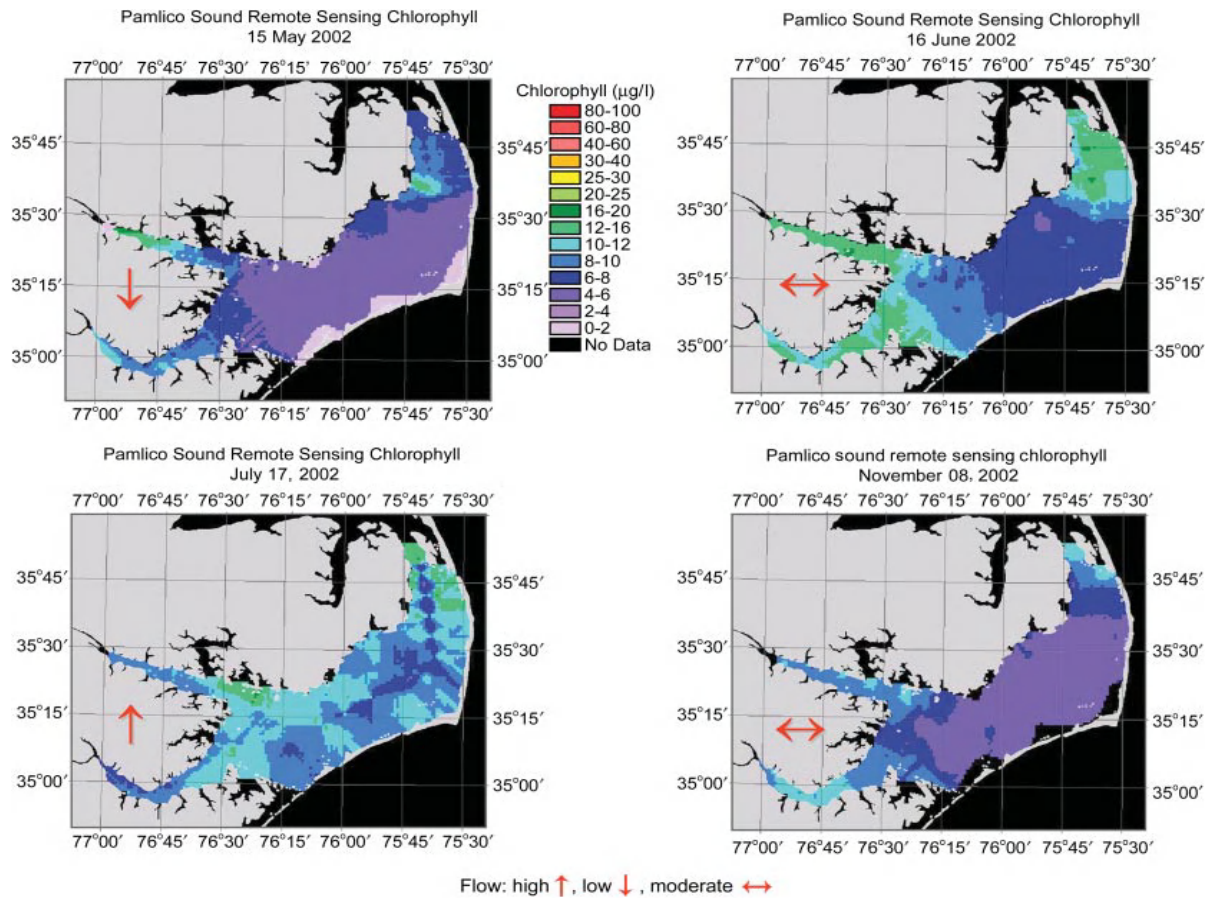
FIGURE 4.2 Spatial relationships of phytoplankton biomass, as chlorophyll *a* (Chl *a*), and freshwater discharge to the Pamlico Sound System, NC. Surface water Chl *a* concentrations were estimated using aircraft-based SeaWiFS remote sensing (Courtesy L. Harding, University of Maryland), calibrated by field-based Chl *a* data. Under relatively low flow, long residence time conditions, phytoplankton biomass is concentrated in the upper reaches of the Neuse and Pamlico R. Estuaries. Under moderate flow, phytoplankton biomass maxima extend further downstream. Under high flow (short residence time), phytoplankton biomass maxima are shifted further downstream into Pamlico Sound. *Source:* Figure adapted from Paerl et al., 2007.
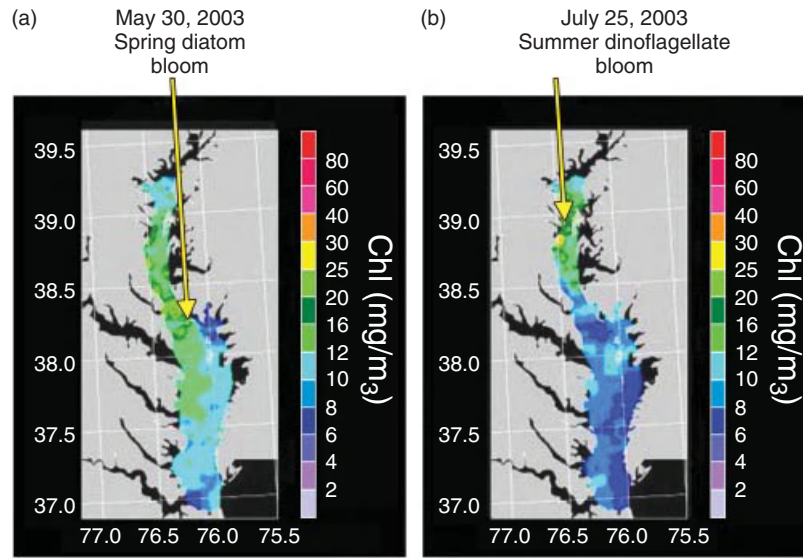
FIGURE 4.3 (a,b) Contrasting spring and summer Chl a distributions in the Chesapeake Bay, during May and July 2003. In May, when flow is high, a large diatom bloom extends into the lower Bay. During lower flow July, a dinoflagellate bloom was observed in the upper Bay. Courtesy of L. Harding, University of Maryland.

as cryptomonads tend to bloom after diatoms, in part because they are capable of maintaining their position in the upper water column once spring diatom blooms have ended and sediment-laden runoff have caused decreases in transparency. Cryptomonads are also quite efficient in sequestering nutrients once diatoms blooms have reduced ambient nutrient levels. During summer months, when freshwater runoff is lowest (and residence time is highest), and nutrients are depleted, temperatures and vertical stratification are high, and slower-growing, highly efficient nutrient-utilizing taxa such as picoplanktonic and N_2 fixing cyanobacterial species exhibit increased dominance.

Lastly, the activities of microzooplankton, macrozooplankton, and benthic invertebrate grazers such as bivalves exert seasonally variable and taxa-specific ''top-down'' controls on phytoplankton community biomass, composition, and succession (Sterner, 1989; Gobler et al., 2002). In addition, microbial interactions, such as bacterial-phytoplankton consortia and symbioses (Paerl and Pinckney, 1996) affect phytoplankton community composition and activity. Grazing and predation seasonally and spatially (along the estuarine salinity gradient) interact with physical and chemical (nutrient) ''bottom-up'' controls on phytoplankton community structure and function. These multiple, interacting controls ensure diversity of phytoplankton functional groups and species in hydrologically and biogeochemically variable coastal ecosystems.

4.4 FACTORS CONTROLLING PHYTOPLANKTON PRODUCTIVITY AND COMMUNITY COMPOSITION

4.4.1 Light

Light is of fundamental importance in controlling the activity, biomass, distribution, and composition of phytoplankton. Phytoplankton use light in the 400–700 nm part of the visible light spectrum. This part of the spectrum is termed *photosynthetically active radiation* or PAR. Both the instantaneous flux of light, or irradiance, and the total amount of light available during daylight tend to be excellent predictors of photosynthetic performance and primary production (Jassby and Platt, 1976). Light availability is controlled by the concentration of key light attenuating substances, turbidity, color, and photopigments (dominated by Chl *a*). Estuarine turbidity may be due to suspended sediments, chlorophyll and other algal photopigments, and colored dissolved organic matter content (Gallegos et al., 1990). Together with surface irradiance, these components determine the attenuation or extinction coefficient K_d. Vertical mixing rates and phytoplankton vertical migration capabilities also strongly affect photosynthetic rates (Mallin and Paerl, 1992). Phytoplankton photosynthetic response to light can be described with photosynthesis–irradiance curves.
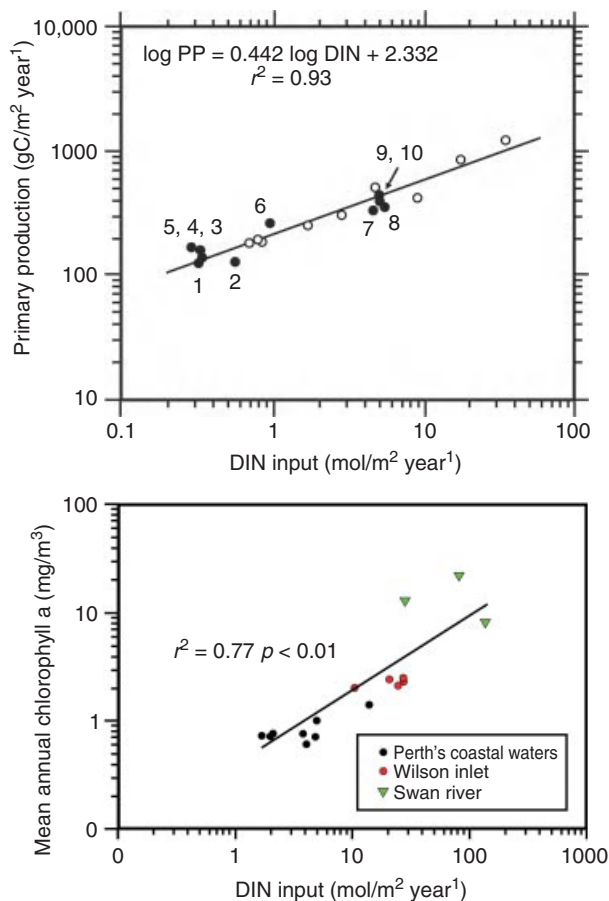
FIGURE 4.4 (a) Relationships between dissolved inorganic N input and primary production in a North American and European estuarine and coastal ecosystems. (b) Relationship between dissolved inorganic N input and phytoplankton biomass, as mean annual chlorophyll *a* content of several Western Australian estuarine systems. *Source:* From Paerl, 2004, Twomey and Thompson, 2001; Nixon, 1980; 1996.

Under natural conditions (e.g., *in situ* bottle incubations), phytoplankton exhibit vertical photosynthetic rate patterns that closely follow the vertical distribution of ambient light. In clear waters and/or under conditions of high surface irradiance, phytoplankton incubated at the water surface frequently experience light inhibition, while maximum rates of photosynthesis usually occur at subsurface depths experiencing from approximately 30% to 70% of surface irradiance. In highly turbid waters, near-surface light inhibition is less common. The depth of maximum photosynthesis depends not only on optimal light but also on adequate nutrient availability and lack of appreciable grazing, which at times can effectively remove phytoplankton at rates exceeding the rate of primary production. Phytoplankton assemblages are adapted to the fluctuating light regimes experienced in well-mixed surface waters (Marra, 1978; Mallin and Paerl, 1992), with maximum rates often occurring under well-mixed conditions. Presumably, mixed conditions ensure that exposure to optimal nutrient and nutrient regimes can be achieved near-simultaneously, enabling cells to maintain high rates of photosynthetic production. Falkowski (1980) showed that under vertically mixed conditions, algal cells can rapidly adapt to changing light and maximize photosynthesis by varying their photosynthetic pigment composition and enzyme concentrations, with response times of 1 h or less. Marra (1978) and Mallin and Paerl (1992) showed that algal cells rotated through a vertical series of depths often had significantly greater photosynthetic production, even though the total light available was the same in both cases. Platt and Gallegos (1980) developed a model simulating phytoplankton photoadaptation to demonstrate that a mixed-water column generated about 20% more photosynthesis than a static system. However, excessive vertical mixing, especially in deeper turbid waters, can be detrimental since it can force phytoplankton into completely dark, aphotic waters, where photosynthesis ceases.

Under vertically stratified conditions, phytoplankton taxa that are able to adjust their position in the water column are frequently at an advantage. They can migrate to and maintain their position at light levels supporting optimal photosynthetic production and growth, while periodically migrating into deeper, nutrient-rich waters to access essential nutrients supplies (Ralston et al., 2007). In particular, near-surface dwelling bloom taxa (some dinoflagellate, cryptophyte, and some cyanobacterial species) use such a strategy to maintain dominance when other factors conducive to bloom formation (elevated temperatures, lack of grazing, optimal flow, and residence time conditions) prevail.

Light is fundamentally important in regulating phytoplankton productivity and nutrient uptake in turbid coastal ecosystems. Cole and Cloern (1984) showed that phytoplankton net production is directly proportional to the ratio of photic zone depth to water column depth for the weakly stratified San Francisco Bay. Mallin and Paerl (1992) and Harding et al. (1985) have shown similar relationships for the Neuse River Estuary, NC, and the Chesapeake Bay. These relationships demonstrate the important interactive roles that clarity and vertical mixing play in regulating primary production and phytoplankton growth, even in very shallow and turbid estuarine ecosystems (cf., Cloern, 1999, 2001). In Long Island Sound and Narragansett Bay, the initiation of the winter–spring diatom blooms is closely related to increasing light

intensities (Riley, 1967; Hitchcock and Smayda, 1977). In North Carolina's Newport River and Neuse River Estuaries, late winter dinoflagellate blooms (*Heterocapsa triquetra*) closely track the increase in light intensities and duration during the winter–spring transition (Paerl et al., 1995; Litaker et al., 2002). Light plays a strong regulatory role with regard to nutrient (specifically nitrogen) uptake and assimilation (Flores et al., 2005), which are energy-dependent processes (cf., Huppe and Turpin, 1994).

4.4.2 Nutrients

Phytoplankton production requires a variety of inorganic and organic nutrients, including carbon (C), nitrogen (N), phosphorus (P), silicon (Si), metals (most importantly iron), and trace elements, as well as vitamins such as B_{12}. The most important are the so-called macronutrients (carbon, nitrogen, phosphorus, and silicon), and among these, nitrogen and phosphorus are most significant, largely because they are usually in shortest supply relative to demand. As a result, availability of these elements controls or ''limits'' the rates of phytoplankton-mediated primary production (Ryther and Dunstan, 1971; Nixon, 1995, 1996). Furthermore, because different algal species require these nutrients in different fixed proportions, the supply ratios of these and other elements (e.g., N/Si and N/Fe) modulate the growth and competitive interactions among phytoplankton taxonomic groups (PTGs; Syrett, 1981; Dortch and Whitledge, 1992; Stolte et al., 1994; Riegman, 1995; Justić et al., 1995; Turner et al., 1998).

Redfield and Daniel (1934) examined the amounts and relative proportions of nutrients in seawater and related these to cellular nutrient content and ratios of the phytoplankton. They found a remarkable consistency in elemental composition of seawater and marine phytoplankton. The ''Redfield ratios'' of atomic weights of the elements C:N:Si:P are in the order of 106:16:15:1. In time and space, however, this balance is not constant. It can be altered by episodic nutrient inputs or depletions from a variety of human and natural sources, which are modulated by and delivered to coastal waters by rainfall and runoff, groundwater, and oceanic inputs. Nutrient delivery to coastal waters generally occurs in a nonsteady, pulsed manner, with several nutrients simultaneously being close to limiting, creating ''colimited'' conditions. Although in estuaries N has been identified as the most limiting nutrient (Ryther and Dunstan, 1971; Nixon, 1995; Granéli et al., 1990; Paerl et al., 1995; Elmgren and Larsson, 2001; Figs 4.4 and 4.5), N and P colimitation is also commonly observed (Boynton and Kemp, 1985; Malone et al., 1996), especially

in the low salinity, upstream segments of estuaries (Fig. 4.6; Fisher et al., 1988; Paerl et al., 1995) and in brackish water deltaic regions where large rivers (e.g., Mississippi) discharge to the coastal ocean (Sylvan et al., 2006). N and P colimitation as well as more exclusive P limitation are most evident during periods of elevated freshwater runoff, which tend to be N enriched (Fisher et al., 1988; Sylvan et al., 2006). Under these conditions, the molar ''Redfield ratio'' of N:P (16:1) can be greatly exceeded, sometimes reaching 200:1, leading to strong P limitation.

Certain phytoplankton groups have highly specific nutrient requirements. The most notable are diatoms, which have siliceous cell walls or frustules. While this provides for strong, morphologically diverse cell walls, it also makes this group reliant on adequate silicon (Si) supplies. Silicon is a product of weathering of upstream siliceous soils. If these soils are absent or sparse, Si supply may be limited. In addition, the supply ratio of Si to other potentially limiting nutrients (N and P) may dictate the relative availability of one or several nutrients in order to maintain (nutrient) balanced or ''Redfield'' growth (Redfield, 1958). Hence, if elevated N and/or P loadings occur as a result of human or climatic perturbations, the supply rate of Si may become limiting, leading to changes in the phytoplankton community composition. This appears to be the case in the northern Gulf of Mexico region where Mississippi River discharge supplies excess N and P relative to Si (Justić et al., 1995; Turner, 2001). Sedimentological evidence indicates that the abundance of the lightly silicified (and hence relatively low Si-requiring) diatom *Pseudonitzschia* has increased since the 1950s, coincidentally with increasing riverine N flux and increasing N:Si ratios (Parsons et al., 2002). Some *Pseudonitzschia* species produce toxins, so Si deficiency could lead to more frequent toxic diatom blooms (Dortch et al., 2001). In addition, because the abundance of copepods decreases when Si:N ratio falls below 1, the diatom-copepod-fish food web may be disrupted under these conditions (Turner et al., 1998; Turner, 2001).

4.4.3 Temperature

The effects of temperature on phytoplankton were provided in an excellent review by Eppley (1972). He noted that temperature–response curves for phytoplankton growth and photosynthesis were similar for most algal species studied, with relatively rapid declines in production at temperatures in excess of their optima. Goldman (1979) showed that temperature optima for five coastal phytoplankton species fell in the range of 20–25 °C. Moreover, it appears that cellular nitrogen content is inversely related
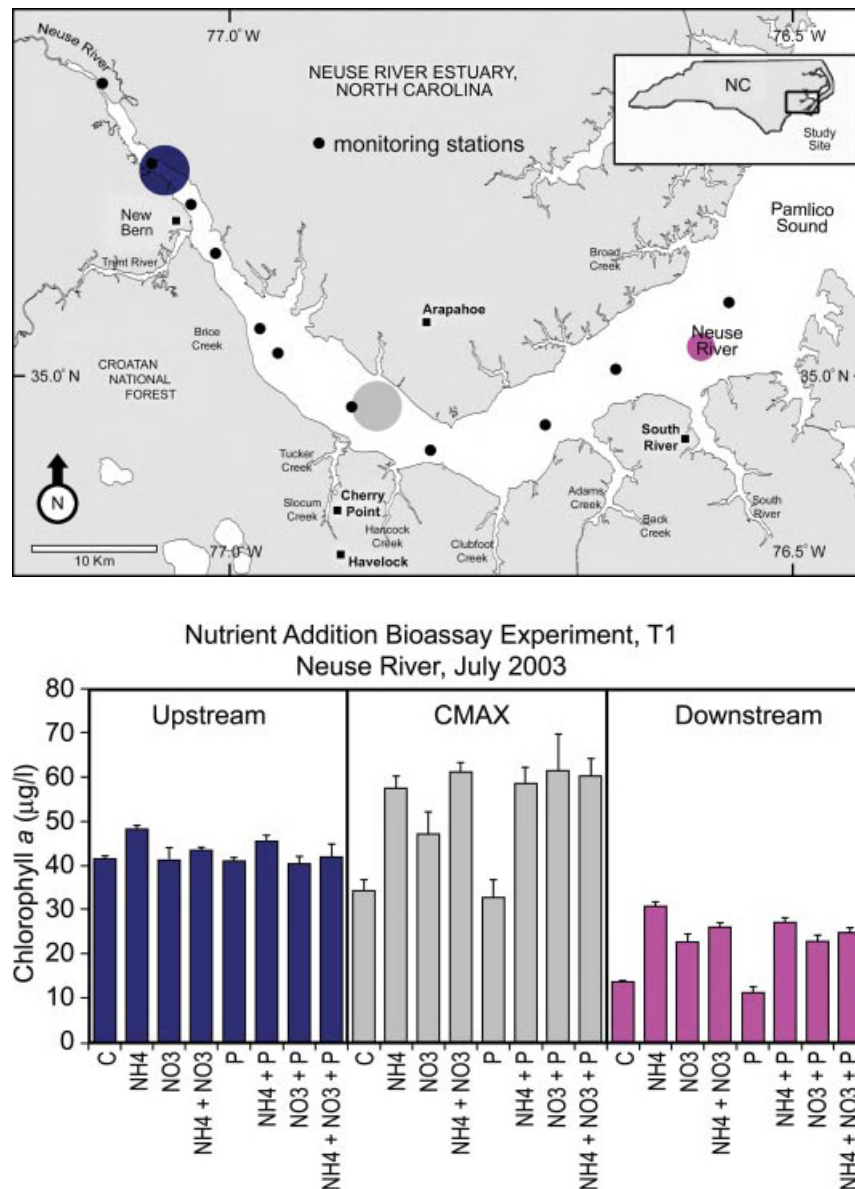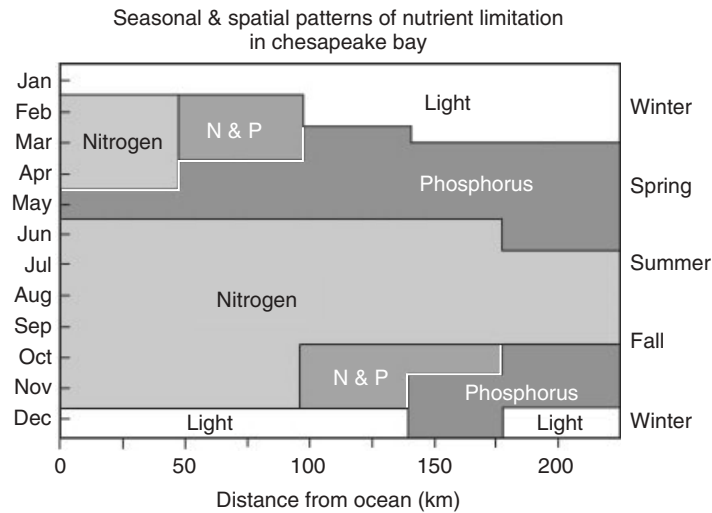
FIGURE 4.5 Results from nutrient addition bioassays conducted at three locations in the Neuse River Estuary, NC. Phytoplankton growth response was measured as accumulation of chlorophyll *a* after 3-day incubation under natural light and temperature conditions. ''C'' indicates controls, in which no nutrients were added. Nitrogen was added as either ammonium (NH_4) or nitrate (NO_3) at 10 µM N concentrations. Phosphorus was added as phosphate (PO_4) at 3 µM P. These summertime bioassays indicate N limitation, which is most profound at more saline downstream locations. Note that per amount of N, ammonium was more stimulatory than nitrate. *Source:* Reprinted from Paerl and Piehler, 2008, with permission from Elsevier.

to the temperature-regulated growth of these algal populations, possibly indicating relatively greater effects of temperature on carbon versus nitrogen metabolism. Temperature evidently exerts a selective force for populations whose temperature optima coincide indirectly with environmental conditions, including vertical stratification, nutrient availability, regeneration, and solubility.

Some phytoplankton taxa are more strongly regulated by temperatures than others. For example, cyanobacterial growth typically exhibits temperature optima in the range of 25–30 °C, which is substantially higher than other phytoplankton groups. The fact that cyanobacteria ''like it hot'' has been linked to an upsurge in cyanobacterial blooms and geographic expansion of such blooms (relative to other

Seasonal & spatial patterns of nutrient limitation in chesapeake bay

FIGURE 4.6 Seasonal and spatial patterns of N and P limitation determined from nutrient addition bioassays conducted on Chesapeake Bay from its relatively fresh headwaters to the saline entrance to the Atlantic Ocean. *Source:* Data from Fisher et al., 1999, actual figure T. R. Fisher, personal communication.

phytoplankton blooms) accompanying regional and global warming (Paerl and Huisman, 2008, 2009).

4.4.4 ''Top-Down'' Control: Herbivory

Zooplankton, benthic filter feeders, larval and certain juvenile, and adult fish are the primary consumers of coastal phytoplankton. The zooplankton are commonly divided into several size classes, that is, microzooplankton (<200 μm), mesozooplankton (0.2–2 mm), macrozooplankton (2–20 mm), and megazooplankton (>20 mm). The relative contributions of these size classes to total phytoplankton biomass can vary substantially. In terms of numbers, the most abundant zooplankters in coastal ecosystems are microzooplankton. This category includes all heterotrophic protists and protozoans. The mesozooplankton includes calanoid copepods, cladocerans, and thaliacean tunicates.

Zooplankton grazing represents an important control of phytoplankton biomass and community composition; however, its impact varies with factors such as seasonality, vertical mixing, freshwater flushing, and residence time. Phytoplankton generally have faster growth rates than zooplankton, which can result in phytoplankton blooms that accumulate more quickly than the zooplankton that graze them. As a result, some rapidly growing bloom taxa can proliferate in a seemingly unabated manner. These blooms are primarily limited by the nutrient supply. This is especially true for phytoplankton species that are capable of blooming during winter and early spring, when water temperatures are too low to support

rapid growth of zooplankton grazers. During these periods, phytoplankton biomass and composition are largely controlled by physical–chemical factors such as light and nutrient availability. This type of control is termed *bottom up*. As water temperatures warm up in spring and summer, zooplankton growth rates are enhanced and biomass can accumulate at faster rates. Also, nutrient supplies to phytoplankton may decrease, largely because the main source of nutrients to the estuary, freshwater runoff, decreases during these drier periods. A result of these combined effects is that herbivorous grazing plays a relatively greater role as a control on phytoplankton biomass. This type of control is termed *top down*. Owing to variable discharge and flow rates as well as other physical factors such as wind-induced mixing, storms, and droughts, there are transitions between periods of low and high grazing control.

Because it is very dynamic and dependent on interacting physical, chemical, and biotic factors, the importance of zooplankton grazing as a control on phytoplankton stocks is a topic that carries a great deal of uncertainty and continues to be hotly debated. Steemann-Nielsen (1958) argued that the commonly observed seasonal patterns of more or less coincidental peaks in phytoplankton and zooplankton abundance supported the hypothesis that grazing maintained algal populations in a steady state, the level of which was determined by the limitations of other environmental conditions (i.e., light, nutrients, and temperature). In contrast, Cushing (1959) used a simple predator–prey model to conclude that

grazing did, indeed, affect the magnitude and timing of phytoplankton stocks and that a lag between peak abundances of phytoplankton and zooplankton populations was readily observable.

High rates of grazer-induced mortality have been observed in coastal environments (e.g., Dagg and Turner, 1982; Welschmeyer and Lorenzen, 1985) and in some river plumes (e.g., Malone and Chervin, 1979). For example, in the northern Gulf of Mexico, the copepod community ingested 4–62% of the daily phytoplankton production (Dagg, 1995a). In a productive subtropical estuary (Fourleague Bay, Louisiana), ingestion rates of phytoplankton by the microzooplankton community averaged 43–165% of the daily phytoplankton production (Dagg, 1995b). In contrast, the grazing contribution from the mesozooplankton, composed primarily of the copepod *Acartia tonsa*, was negligible, presumably because of high advective losses and predation by zooplanktivorous fish (Dagg, 1995b).

While zooplankton herbivory may be an important control on coastal phytoplankton production during certain seasons under certain environmental conditions (Martin, 1970), it is not likely to be a severe limitation overall (e.g., Oviatt et al., 1979). Often, grazing is insufficient to balance phytoplankton growth, which can lead to the development of phytoplankton blooms. In Chesapeake and Narragansett Bays, high rates of suspension-feeding rates by ctenophores and medusae on zooplankton may serve to keep zooplankton grazing in balance (Heinle, 1974; Kremer, 1979). Other studies show inverse relationships between abundances of herbivorous crustacean and gelatinous zooplankton from field observations and direct relationships between ctenophore abundance and phytoplankton chlorophyll *a* (Lindahl and Hernroth, 1983; Feigenbaum and Kelly, 1984).

In some estuaries, suspension-feeding benthic macrofauna can reduce phytoplankton abundance significantly (Cloern, 1982; Officer et al., 1982). For several estuarine systems, it has been shown that a single dominant suspension-feeding bivalve population was capable of filtering the entire overlying water column in 1–4 days (Cohen et al., 1984; Nichols, 1985; Doering et al., 1986). Such grazing rates can reduce phytoplankton standing stocks significantly. For example, the invasion of zebra mussels (*Dreissena polymorpha*) caused a massive decline in phytoplankton biomass in the Hudson River Estuary (Caraco et al., 1997). Zebra mussels invaded this estuary in 1992 and became well established in 1993 and 1994. During these 2 years, the grazing pressure on phytoplankton increased 10-fold, leading to an 85% decline in phytoplankton biomass (Caraco et al., 1997).

4.5 HUMAN AND CLIMATIC IMPACTS ON COASTAL PHYTOPLANKTON DYNAMICS

4.5.1 Effects of Nutrient Overenrichment on Estuarine Phytoplankton

Coastal primary production and phytoplankton biomass are strongly controlled by the availability and supply rates of nutrients, especially N (Nixon, 1995; Boesch et al., 2001; Paerl and Piehler, 2008) and to a lesser extent P (Sylvan et al., 2006). There is a delicate balance between beneficial nutrient enrichment to sustain a productive and healthy food web, and overfertilization, which can greatly accelerate primary production and promote excessive organic matter production (i.e., eutrophication; Nixon, 1995). If not effectively utilized by the food web, excess organic matter can accumulate, leading to water quality problems and habitat degradation (Fig. 4.7).

Symptoms of eutrophication include phytoplankton blooms, loss of submerged aquatic vegetation, severe oxygen depletion (hypoxia), and fish kills (Paerl, 1988, 2004). Sudden changes in temperature, nutrient depletion, and light availability constraints can cause blooms to die (Paerl, 1988). When blooms die, they sink into deeper waters, where they decompose (Fig. 4.7). This process consumes vast amounts of oxygen, and if deep waters are not mixed with oxygen-rich surface waters, they eventually run out of oxygen, creating hypoxia, which can suffocate finfish and shellfish. Nutrient-stimulated hypoxia is a major cause of habitat loss and finfish and shellfish kills (Diaz and Rosenberg, 2008).

Rapidly expanding urban, agricultural, and industrial activities in coastal watersheds have greatly accelerated the production and delivery of nutrients to nutrient-sensitive estuarine and coastal waters. Anthropogenic and natural sources of N and P are delivered by (i) surface water discharge delivered via creeks and rivers, (ii) subsurface discharge (groundwater), and (iii) atmospheric deposition (rainfall or dry fall, mainly as N). The proportions of these nutrient sources vary geographically and demographically. In rural, agriculturally dominated regions, 50% to over 75% of N and P input originates from diffuse, nonpoint sources such as surface runoff, rainfall, and groundwater (Paerl, 1997; Howarth, 1998; Boesch et al., 2001; Moore, 1999). Point sources, including wastewater, industrial, and municipal discharges, account for the rest. In contrast, N and P loading in urban watersheds (e.g., Narragansett Bay and Puget Sound) are dominated (>50%) by point sources,
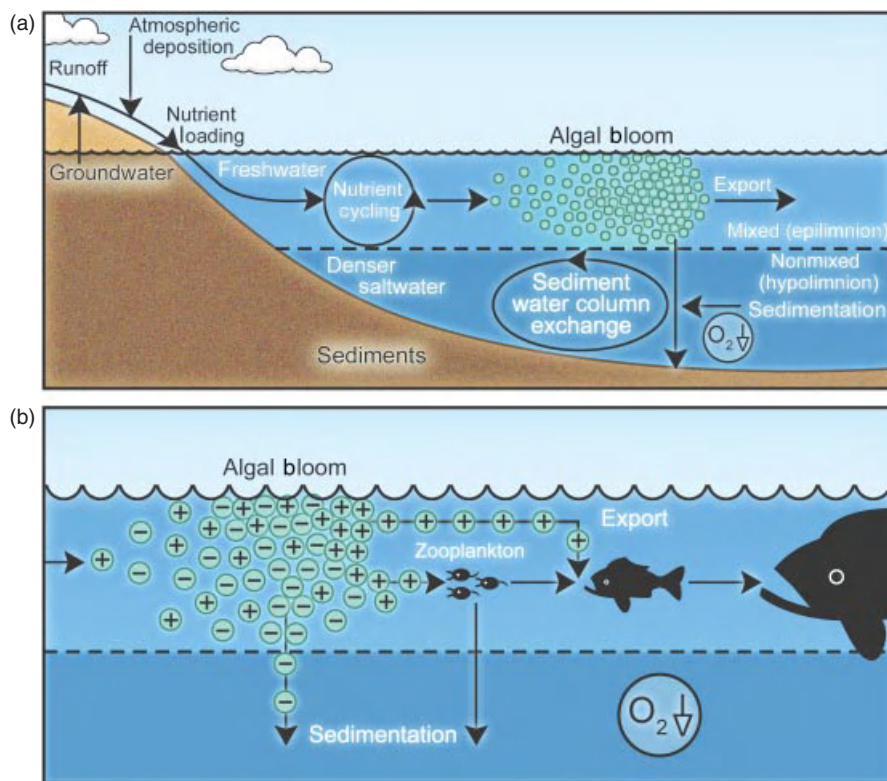
FIGURE 4.7 (a) Linkage between external nutrient loading, internal nutrient cycling, nutrient-enhanced algal bloom formation, and hypoxia under salinity-stratified conditions. (b) Differential impact on hypoxia of phytoplankton species that are readily consumed (labeled +) versus species that are not (−). Species that are not consumed form a larger share of sedimented organic matter and represent a larger burden on the ecosystem hypoxia potential of the estuary. *Source:* From Paerl, 2003.

while watersheds encompassing both urban centers and intensive agriculture (e.g., Chesapeake Bay and San Francisco Bay regions) exhibit a more even distribution of these source types (Castro et al., 2003).

4.5.2 The Roles of Climatic Variability in Eutrophication Dynamics

Nutrient, sediment, and other contaminants in coastal waters are strongly influenced by climatic forcing features, especially freshwater discharge, the main delivery mechanism. Climatic shifts, including increasing tropical storm and hurricane frequencies (Goldenberg et al., 2001; Webster et al., 2005) and changing drought conditions, accelerate these inputs. It is therefore useful to develop ecological indicators that could help distinguish human impacts from natural perturbations. This goal is compounded by the fact that human and natural perturbations may be identical, overlap, or act synergistically, potentially blurring this distinction.

Data from the mid-1990s to present show that many coastal systems have experienced the combined stresses of anthropogenic nutrient enrichment,

droughts (reduced flushing combined with minimal nutrient inputs), and elevated tropical cyclone activity (high flushing accompanied by elevated nutrient inputs). These distinct perturbations have proved useful for examining impacts of anthropogenic and natural stressors on phytoplankton community structure. Seasonal and storm-induced variations in river discharge, which affect flushing and residence times, strongly affect competition and relative dominance among different PTGs, as a function of their contrasting growth rates and doubling times. For example, the relative contribution of chlorophytes, cryptophytes, and diatoms to the total Chl *a* pool appeared strongly controlled by periods of elevated river flow in North Carolina's Neuse River Estuary and downstream Pamlico Sound (Fig. 4.8; Valdes-Weaver et al., 2006; Paerl and Huisman, 2009).

These effects are most likely due to differential nutrient uptake and growth rates among PTGs (Pinckney et al., 1999). Cyanobacteria, which generally have slower growth rates, were more abundant when flushing was minimal (i.e., longer residence times) during summer (Fig. 4.8). Historic trends in dinoflagellate and chlorophyte abundance provide
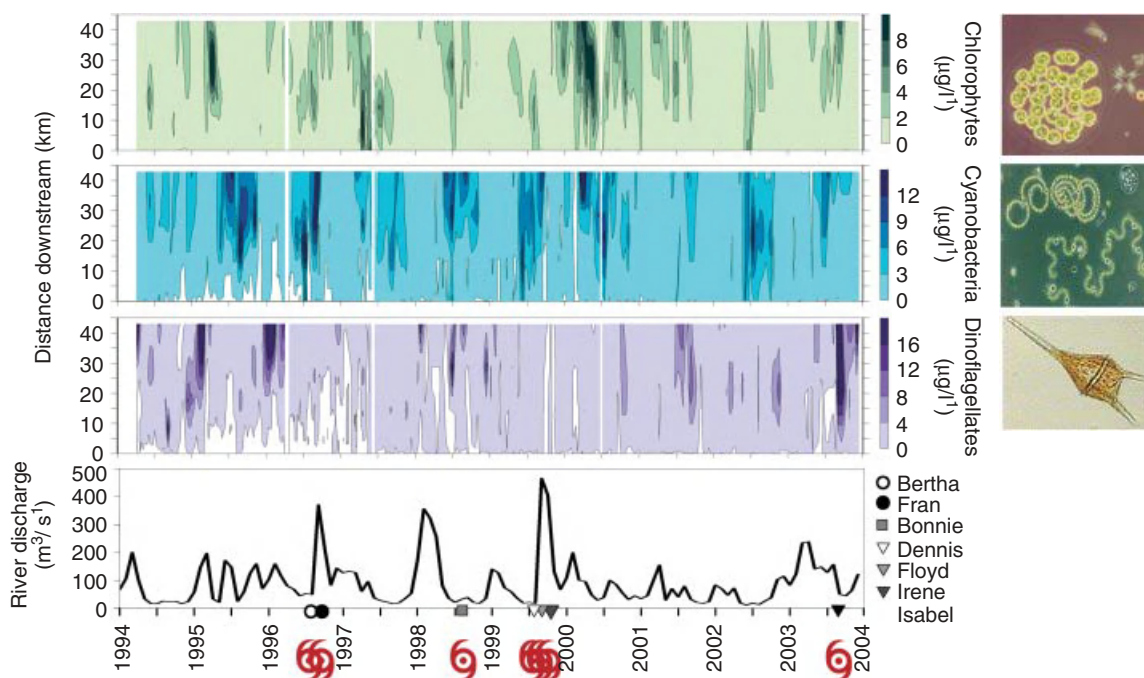
FIGURE 4.8 Phytoplankton taxonomic group biomass responses, based on diagnostic (of algal taxonomic groups) photopigment measurements, to flow and nutrient enrichment in the Neuse River Estuary during 1994–2004. Shown here are responses for chlorophytes (green algae), cyanobacteria (blue-green algae), and dinoflagellates. Note the strong stimulatory responses of chlorophytes to high discharge following major hurricanes (1996 and 1999) and periods of high spring runoff (spring 1998). In contrast, the relative contributions of dinoflagellates to phytoplankton community biomass decreased during periods of high flow. Cyanobacterial biomass contributions decreased during high flow, but recovered noticeably during subsequent summer low flow periods. *Source:* Adapted from Paerl et al., 2006b.

additional evidence that hydrologic changes have altered phytoplankton community structure in the Neuse River estuary. Both decreases in the occurrence of winter–spring dinoflagellate blooms and increases in the abundance of chlorophytes coincided with the increased frequency and magnitude of hurricanes since 1996 (Fig. 4.8; Paerl et al., 2006a,b; Valdes-Weaver et al., 2006). The relatively slow growth rates of dinoflagellates account for their reduced abundance during the ensuing high river discharge events. Overall, phytoplankton composition has been altered since 1994 following major hydrologic changes, specifically flooding from large hurricanes such as Fran and Floyd (Paerl et al., 2005, 2006b). These phytoplankton community changes signal potential trophic and biogeochemical alterations.

There is a scientific consensus that the buildup of greenhouse gases in the atmosphere is warming the earth (Houghton et al., 2001, see also Chapter 20). The past decade was the warmest since temperature records began in 1850, and paleo-records indicate that recent warming has no counterpart in the past 1000 years (Crowley, 2000). The global Earth's temperatures increased by almost $1\,^{\circ}C$ during the past

150 years (Jones et al., 1999), and general circulation models have projected further temperature increases of 1–$6\,^{\circ}C$ over the next 100 years (Houghton et al., 2001). A global circulation model-based study that examined the impacts of global warming on the annual runoff of the world's 33 largest rivers (Miller and Russell, 1992) suggested that runoff increases are likely for 25 of the 33 studied rivers. Under this scenario, the average annual Mississippi River discharge would increase 20% if the concentration of atmospheric CO_2 doubles. Other studies have shown that runoff estimates for the Mississippi River Basin differed greatly between the Canadian model and the Hadley model (Wolock and McCabe, 1999). Both models predict an increase in future extreme rainfall and runoff events, but they disagree in terms of both the magnitude and direction of changes in average annual runoff. The average annual runoff of the Mississippi River Basin, for example, was projected to decrease 30% for the Canadian model but increase 40% for the Hadley model by the year 2099. Estimated changes into major US estuaries projected by the Hadley model by the year 2099 range from -40%
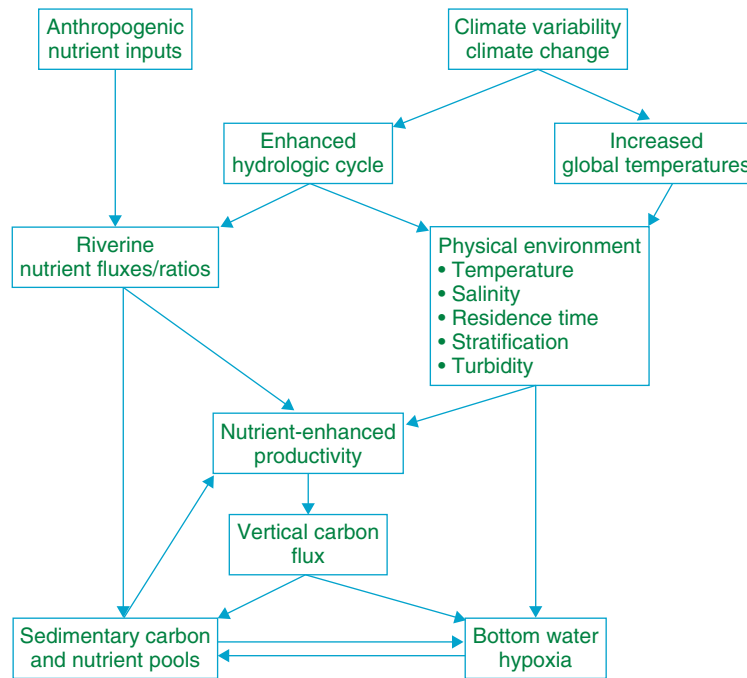
FIGURE 4.9 Coupling between climate variability, coastal eutrophication, and hypoxia. *Source:* Reprinted from Justić et al, 2005, with permission from Elsevier.
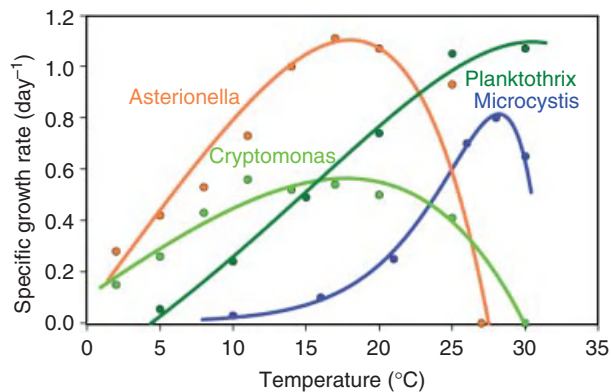
FIGURE 4.10 Temperature dependence of the specific growth rates of two bloom-forming cyanobacteria *Microcystis aeruginosa* (Reynolds, 2006) and *Planktothrix agardhii* (Foy et al., 1976), the diatom *Asterionella formosa* (Butterwick et al., 2005), and the cryptophyte *Cryptomonas marssonii* (Butterwick et al., 2005). The data are from controlled laboratory experiments using light-saturated and nutrient-saturated conditions. Solid lines are least-squares fits of the data to the temperature–response curve of Chen and Millero (1986).

that many coastal and estuarine ecosystems will experience changes in freshwater inflow, although it is unclear in what manner these changes will occur. It is also likely that extreme precipitation events will become more common, as may droughts and floods (Easterling et al., 2000).

Increased global temperatures, combined with an enhanced hydrologic cycle, may influence estuarine and coastal eutrophication in three major ways (Fig. 4.9). First, the magnitude and seasonal patterns of freshwater and nutrient inputs would be affected, which could affect nutrient-enhanced coastal productivity. Second, altered flushing and residence times would affect phytoplankton competitive interactions and hence dominance among major taxonomic groups. Third, increases in air and hence water temperatures will have a direct effect on phytoplankton physiology and growth. For example, cyanobacteria generally prefer much higher temperatures for optimizing growth than other taxonomic groups (e.g., diatoms, cryptophytes, and chlorophytes; Fig. 4.10). Thus, in a warmer world, cyanobacterial growth and possibly bloom formation would be enhanced relative to other competitive taxonomic groups. Such taxonomic shifts would have ramifications for food web and nutrient cycling dynamics (Paerl and Huisman, 2008, 2009).

to +100%. Similar calculations based on the Canadian model projections suggest significantly reduced inflows for all coastal regions except the US Pacific coast (Wolock and McCabe, 1999). Thus, it is likely

FIGURE 4.11 Algal blooms in representative estuarine and coastal waters. (a–c) Cyanobacterial bloom in the St. John's River Estuary, Florida (Courtesy J. Burns); dinoflagellate red tide, coastal Pacific Ocean, Japan (Courtesy ECOHAB Program); cyanobacterial bloom in the lagoonal Neuse River-Pamlico Sound, North Carolina (photo: H. Paerl). (d–f) Mixed algal bloom, Orielton Bay, Australia (Courtesy Commonwealth Scientific and Industrial Research Organisation, CSIRO-Australia); near-shore dinoflagellate bloom, W. Florida (Courtesy Florida Department of Environmental Protection); cyanobacterial bloom, Lake Ponchartrain, Louisiana (Courtesy J. Burns). (g–i) Cyanobacterial bloom in the Baltic Sea near the Finnish coast (Courtesy Finnish Border Guard and Finnish Marine Research Institute); dinoflagellate bloom, Pamlico Sound, North Carolina (Courtesy P. Tester, National Oceanographic and Atmospheric Administration, NOAA); dinoflagellate red tide, in coastal waters near Hong Kong (Courtesy K. Yin).

4.6 HARMFUL ALGAL BLOOMS

Phytoplankton blooms are a rapid and perceptible increase in phytoplankton biomass in an aquatic ecosystem (Fig. 4.11). As discussed above, bloom initiation and persistence is a complex environmental issue that involves specific circulation and current patterns, nutrients, light, herbivory, and other factors. Blooms may produce biotoxins, cause hypoxia, and alter food webs; in each case, they can constitute an environmental health hazard, degrade water quality and habitat, and are therefore deemed ''harmful algal blooms'' (HABs; Table 4.1). Species in diverse phytoplankton groups can be HABs, including cyanobacteria, dinoflagellates, prasinophytes, and diatoms. During blooms, fish and shellfish may consume these algae, then accumulate and concentrate the biotoxins without apparent harm. This renders the fish and shellfish extremely toxic to whomever consumes them, including marine mammals, sea birds, and humans. In places where HAB monitoring and surveillance programs do not exist, these blooms may go unnoticed until they cause illnesses and/or death in humans who consume products from the sea.

4.7 NUTRIENT MANAGEMENT OF PHYTOPLANKTON PRODUCTION AND COMPOSITION

When controlling and managing the effects of excessive nutrient loading on estuarine and coastal

TABLE 4.1 Economic and public health problems related to coastal harmful algae in the United States

- Paralytic shellfish poisoning (PSP), which occurs in all coastal New England states as well as New York and along much of the west coast from Alaska to California. This problem has also extended to offshore areas in the northeast (causative species—the dinoflagellates *Alexandrium tamarense, Alexandrium fundyense*, and *Alexandrium catenella*)
- Neurotoxic shellfish poisoning (NSP) and fish mortalities in the Gulf of Mexico and, more recently, extending along the Atlantic Coast from Florida to the Carolinas (causative species—the dinoflagellate *Karenia brevis*)
- Mortalities of farmed salmonids in the Pacific Northwest (causative species—the diatoms *Chaetoceros convolutus* and *Chaetoceros concavicornis* and the raphidophyte *Heterosigma akashiwo*)
- Recurrent brown tides causing mass mortalities of mussel populations in Rhode Island, massive recruitment failure of scallops, and reduction in eelgrass beds around Long Island (causative species—the previously unknown chrysophyte, *Aureococcus anophagefferens*)
- Ciguatera fish poisoning (CFP), a malady associated with dinoflagellate toxins accumulated in tropical fish flesh, occurring in virtually all subtropical to tropical US waters (Florida, Hawaii, Guam, US Virgin Islands, Puerto Rico, Guam, and other Pacific Territories; major causative species *Gambierdiscus toxicus, Prorocentrum* spp., *Ostreopsis* spp., *Coolia monotis, Thecadinum* sp., and *Amphidinium carterae*)
- Amnesic shellfish poisoning (ASP), which occurred first in southeastern Canada in 1987, but has been a problem for the US Pacific coast states over the past 2 years (causative species—the diatoms *Pseudonitzschia pungens* forma *multiseries* and *Pseudonitzschia australis*). This sometimes fatal illness is so named because one of its most severe symptoms is permanent loss of short-term memory. The ASP toxin, domoic acid, has been detected in shellfish from both the West and East Coasts of the United States, and toxic *P. pungens* f. *multiseries* cells have been isolated from Gulf of Mexico waters, although a toxin has yet to be detected in the field. The threat to US shellfish consumers from this alga covers a broad geographic area. The name ''ASP'' understates the severity of the problem, since domoic acid also accumulates in fish and in crab viscera along the west coast of the United States, where the impact of this toxin on nonmolluscan fisheries may well exceed the loss to molluscan fisheries (e.g., razor clam)
- Diarrhetic shellfish poisoning (DSP), which some consider the most serious and globally widespread phytoplankton-related seafood illness. Major causative species are dinoflagellates *Dinophysis* and *Prorocentrum*. The first confirmed incidence of DSP in North America occurred in 1990 when these toxins were detected in shellfish from the southern coast of Nova Scotia following numerous human illnesses. Another DSP outbreak in Canada occurred in 1992. DSP-producing phytoplankton species occur throughout all temperate coastal waters of the United States, and thus present a potential problem for the future, although no outbreaks of DSP have yet been confirmed
- Cyanobacteria blooms are becoming more numerous, widespread, and persistent in nutrient-enriched estuarine and coastal waters worldwide. Blooms have multiple negative impacts, such as toxicity, overgrowing, and smothering seagrasses, coral reefs and shellfish habitats, and food web shifts. Some species produce toxins and other bioactive metabolites. Of concern are blooms of toxic heterocystous N_2 fixing genera *Nodularia* (full salinity) and *Cylindrospermopsis* (oligohaline). The filamentous, nonheterocystous N_2 fixing species *Lyngbyamajuscula* produces both dermatotoxins and neurotoxins. Blooms of this subtropical/tropical species have fouled large segments of both Hawaii and Florida's estuaries and bays. Some tropical harmful cyanobacterial species are speaking into more temperate regions in part due to global warming, which has expanded their habitat (Paerl and Huisman, 2008)

Source: In part adapted from Anderson et al. (2000).

eutrophication and HAB development, anthropogenic point and nonpoint sources are the most significant targets for nutrient reduction. The amounts, forms, and relative proportions of nutrients vary according to human activities, locations, and distributions of population centers and routes of nutrient discharge (i.e., surface, subsurface, and atmospheric). Magnitudes and proportions of N and P input have been shown to control both phytoplankton community productivity and compositional responses in receiving waters (Smith, 1990), and as

such both aspects require careful assessment and management. In point source-dominated watersheds, the emphasis has been on improved wastewater (from sewage and industrial effluent) treatment and removal of both N and P. In nonpoint source-dominated watersheds, surface runoff, especially that originating from agricultural operations and urban stormwater, are the prime focus of N reduction strategies. These strategies include best management practices, including prudent and timely applications of fertilizers, soil conservation, establishment of
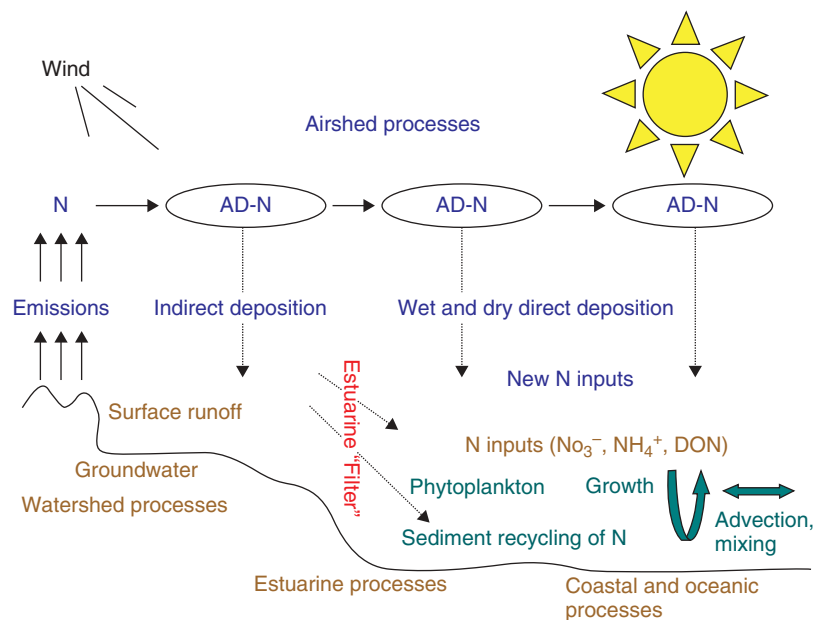
FIGURE 4.12 Illustration of the estuarine ''filter'' concept, where land-based nitrogen (N) nutrients are filtered by the estuary, while some portion of atmospheric N deposition bypasses the ''filter,'' directly fertilizing coastal and oceanic waters.

riparian vegetative buffer zones, and use of wetlands to enhance ''stripping'' of runoff-based N (Mitsch et al., 2001).

Both N and P point sources are under intense local, state, and federal scrutiny. Recent agency (e.g., US-Environmental Protection Agency-EPA, 1998, 1999, European Parliament: European Economic Union-EEU-Water Framework, 2003) and legislative action has led to strict N and P discharge limits from wastewater treatment plants, and those plants not able to meet these standards are under considerable and continuing pressure to upgrade. In addition, a phosphate detergent ban was enacted in the mid-1980s in North America, Europe, and parts of Australasia. This has led to marked decreases in P loading in many watersheds. Current strategies aimed at reducing nonpoint N discharge, including riparian buffers, wetland construction, and soil conservation, also retard the movement of P to nutrient-sensitive waters. Therefore, the primary strategies and targets for pursuing N input constraints will yield significant parallel reductions in P.

In addition to surface runoff, atmospheric deposition and groundwater should also be recognized as significant sources of new N potentially stimulating primary production in estuarine and coastal waters (Paerl, 1985, 1997). Local and regional studies have shown atmospheric deposition and groundwater inputs of N to be large, increasing, and of widespread importance in estuarine and coastal environments (Jaworski et al., 1997; Paerl and Whitall, 1999; Valigura, 2001; Paerl et al., 2002). For example, along the US Eastern seaboard, atmospheric deposition accounts for 10% to over 30% of externally supplied N sources (Paerl et al., 2002; Castro et al., 2003). Atmospheric deposition plays an increasingly important role in coastal waters, since surface runoff N is often effectively ''filtered'' in N-limited estuarine systems as it transits to the ocean (Paerl and Whitall, 1999). Atmospheric deposition as well as groundwater can be directly discharged to coastal waters and bypass this estuarine N filter (Paerl et al., 2002; Moore, 1999; Fig 4.12). It has been suggested that these N inputs may be key drivers of a reported recent increase in HABs in coastal waters (Paerl, 1997; Richardson, 1997). This, combined with observations that N and P loading to these waters has increased steadily in comparison to silicon (Si), may also help explain observed shifts in phytoplankton community away from Si-requiring diatoms to flagellates, dinoflagellates, and cyanobacteria (Dortch and Whitledge, 1992; Riegman, 1995).

Certain forms of N may be preferred by phytoplankton, including bloom-forming species. For example, in highly turbid estuarine waters where light availability may be limited, N sources that require the least amount of energy for uptake and assimilation may be preferred. This means that under these conditions, the most readily assimilated and least energy-requiring form of N, ammonium, may be

preferred over the oxidized forms nitrite and nitrate (Harrison and Turpin, 1982). Experimental work has confirmed this for nutrient-enriched estuarine and coastal waters (Syrett, 1981; Collos, 1989; Stolte et al., 1994; Riegman, 1995). In addition, some phytoplankton groups and species are more capable than others at utilizing organic forms of N and other nutrients (Paerl, 1988; Antia et al., 1991). These findings stress the need for considering both the qualitative and quantitative influences of N (and other nutrient) loadings on phytoplankton biomass and compositional responses.

An additional challenge for managing estuarine primary production and phytoplankton community composition is the influence of climate change. Some symptoms of climate change, such as increased tropical storm activity, larger oscillations between extremely wet and drought conditions, and hence the more pulsed, episodic manner in which nutrients are supplied to coastal ecosystems, can confound management strategies that are based on average or "normal" hydrologic and nutrient discharge patterns. Since entering the recent period of elevated hurricane activity (Goldenberg et al., 2001), it seems that episodicity is now the norm rather than the exception. This calls for highly adaptive nutrient management strategies that take pulsed instead of more gradual patterns of nutrient and other pollutant input in consideration.

Much work lies ahead to further identify, characterize, and manage nutrient inputs controlling phytoplankton production and composition in estuarine and coastal waters. Research and monitoring are providing information essential for formulating long-term nutrient management strategies aimed at protecting and preserving the high standards of water quality and resourcefulness that we expect. With respect to phytoplankton production and composition needed to sustain desirable estuarine and coastal food webs, this means managing for enough, but not excessive production, and avoiding the promotion of harmful taxa. As we enter the new millennium, fostering a process-based understanding of nutrient–water quality interactions and utilizing this for effective management are key social, economic, and political responsibilities as we ensure long-term conservation and sustainability of coastal waters.

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SEAGRASS AND RELATED SUBMERSED VASCULAR PLANTS

Jens Borum, Renee K. Gruber, and W. Michael Kemp

5.1 INTRODUCTION AND DESCRIPTION

Seagrass and other submersed vascular plants are characteristic and often quantitatively important primary producers in estuarine areas. While the diversity of the truly marine macrophyte communities composed by red, green, or brown macroalgae is high with numerous species, size classes, and growth forms, a limited number of species of submersed plants can grow and survive in marine areas (Fig. 5.1). Almost all species are monocotyledonous flowering plants. Some of the species are actually freshwater plants able to tolerate only low salinity conditions, and they are restricted to the upper reaches of the estuaries. Close to river outlets, one may find *Elodea canadensis, Myriophyllum spicatum*, and *Vallisneria americana* (0–10 salinity), while *Zannichellia palustris, Potamogeton perfoliatus*, and *Stuckenia pectinata* can form dense stands in areas with slightly higher salinity (up to 15).

Only between 50 and 60 species of submersed vascular plants tolerate, and typically prefer, full-strength seawater. These plants, referred to as *seagrasses* (den Hartog, 1970), belong to two major botanical families, Potamogetonaceae and Hydrocharitaceae, which are divided into 12 genera. The seagrasses are morphologically quite diverse ranging from small shoots (*Halophila* spp., 3–5 cm) with elliptic leaves to larger plants (*Zostera* spp. and *Enhalus*, up to 2 m long) with broad (up to 2 cm), linear leaves. All species have below-ground rhizomes from which root and leaf bundles are formed. Many freshwater vascular plants have apical meristems that enable them to grow toward the light at the surface. In contrast, all seagrasses have basal leaf meristems that allow continuous replacement of old epiphyte-covered leaves with new clean leaves.

The submersed vascular plants that inhabit estuarine waters have terrestrial and freshwater ancestors that had invaded the marine environment at different times during their evolution. As the diversity in morphology of seagrasses suggests, the seagrasses had invaded the marine environment on more than one instance (Les et al., 1997). Accordingly, they have different origins and are referred to as a *polyphyletic group*, where some species are more closely related to freshwater species than to other seagrass species.

5.1.1 Challenges and Benefits of Aquatic Life for Submersed Vascular Plants

The reinvasion of the aquatic environment by terrestrial plants created a number of challenges and benefits for plant survival. Terrestrial plants are susceptible to desiccation, but this is obviously not a
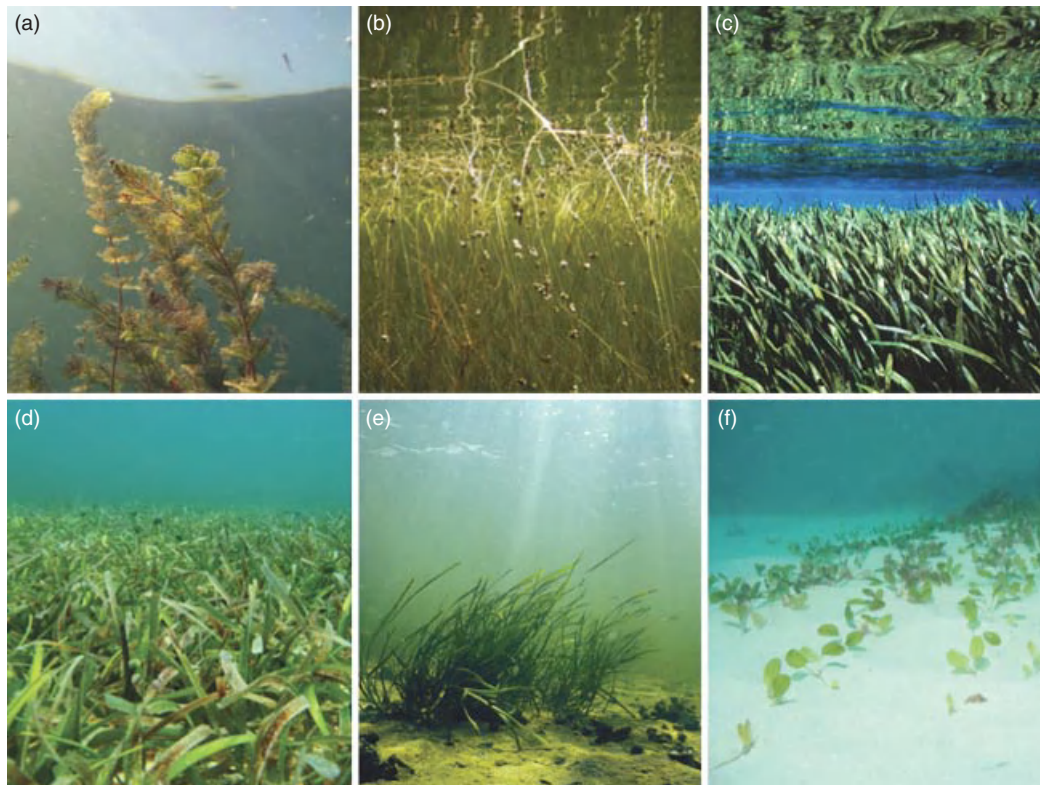
FIGURE 5.1 Examples of submersed vascular plants that occur in estuarine systems: (a) *Myriophyllum spicatum* (photo: O. Pedersen), (b) *Stuckenia pectinata* (photo: O. Pedersen), and (c) *Vallisneria americana* (photo: Seafavorites.com) are freshwater plants that are able to tolerate low salinities (<15), while (d) *Thalassia testudinum* (photo: O. Pedersen), (e) *Zostera marina* (photo: P.B. Christensen; NERI), and (f) *Halophila ovalis* (photo: P. Lavery) are seagrasses that thrive in full-strength seawater.

problem for submersed plants. Submersed plants have lost most of the physiological protections used by land plants to guard against desiccation such as hairs or other leaf structures, and the leaf cuticle of submersed plants is greatly reduced. One advantage of this evolutionary change is that nutrients, apart from being taken up by the roots, can be extracted rather efficiently from the water column when the cuticle on the leaves is thin (Hemminga and Duarte, 2000). On the other hand, submersed plants lack the ability to transpire from leaves, which is a process used by terrestrial plants to drive internal transport of water along with nutrients and organic compounds. In submersed plants, internal mass transport of solutes is instead provided by creation of root pressure, which is an energy-consuming process (Pedersen and Sand-Jensen, 1993).

Terrestrial plants often have a considerable number of structural tissues to strengthen stems and leaves. Submersed plants have lost this ability, and instead maintain their structure with air-filled lacunae, making leaves buoyant. They also have flexible leaves constructed with materials that are strong enough to tolerate the drag forces induced by waves and currents (Koch, 2001).

The supply of inorganic carbon to fuel photosynthesis represents a major problem for submersed vegetation (Madsen and Sand-Jensen, 1991; Beer and Koch, 1996). Carbon dioxide is readily dissolved in water, but the diffusion of CO_2 through the stagnant boundary layer around leaf surfaces is very slow compared to that in air because the diffusion coefficients of gases in air are about 10,000 times faster than in water. Therefore, as described later, many submersed plants have developed the ability to use inorganic carbon in the form of bicarbonate (HCO_3^-), which is about 100 times more abundant than dissolved CO_2 in seawater.

Another physiological challenge for submersed plants is the fact that below-ground tissues are often situated in anoxic sediments (Armstrong, 1979). If the internal oxygen supply to rhizomes and roots is insufficient, the tissues must temporarily rely on anaerobic metabolism, which is an inefficient source of energy and which generates toxic anaerobic metabolites such as lactate or ethanol (Raven and Scrimgeour, 1997).
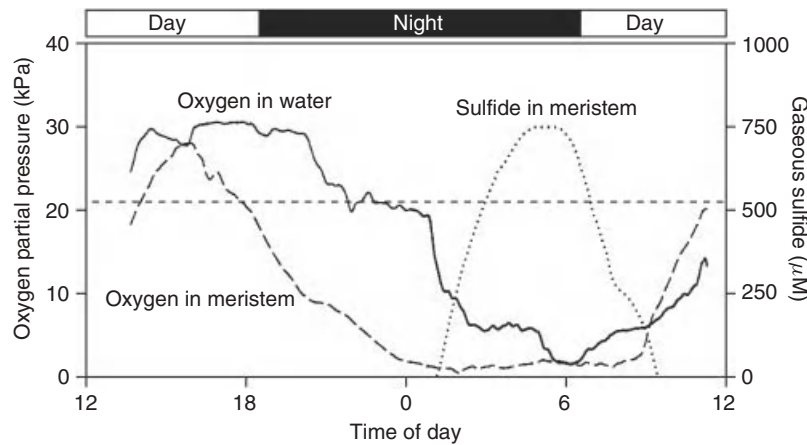
FIGURE 5.2 One of the most serious physiological challenges for submersed vascular plants is to supply rhizomes and roots with sufficient oxygen to support aerobic metabolism and prevent invasion of anaerobic metabolites from the sediment. The figure shows how internal plant oxygen and gaseous sulfide, measured with microelectrodes, interact over a diel cycle in a *T. testudinum* bed in Florida Bay, USA, during a seagrass die-off period. The oxygen within the plant meristem changed from supersaturation (i.e., above the oxygen partial pressure of the atmosphere indicated by the stippled line) during daytime to very low levels at night, when water column oxygen content was low. When plant oxygen is low, poisonous sulfide can invade from the sediment into the plant as seen shortly after midnight on this occasion. *Source:* Redrawn after Borum et al. (2005).

The final, and maybe the most serious challenge to submersed plants, at least in the sulfate-rich marine environment, is that highly toxic sulfide, which is produced by microbial sulfate reduction in sediments, may invade plant tissues during conditions of anoxia (Fig. 5.2; Carlson et al., 1994; Raven and Scrimgeour, 1997; Pedersen et al., 2004). The combined effect of plant anoxia and sulfide invasion may be responsible for periodic massive plant mortality as has been suggested for turtlegrass (*Thalassia testudinum*) in Florida Bay (Robble et al., 1991; Zieman et al., 1989; Borum et al., 2005) and for eelgrass (*Zostera marina*) in Europe (Plus et al., 2003).

5.1.2 Spatial Distributions

The global geographical distribution of submersed vascular plants in estuaries varies substantially among species. Some are confined to very restricted geographic areas, such as *Posidonia oceanica* in the Mediterranean Sea, while seagrass species belonging to the genus *Zostera* are widely distributed in both the southern and northern temperate zones of Asia, Europe, Africa, and North America (den Hartog, 1970). There are no submersed plants in Antarctica, but *Z. marina* is found in the Arctic areas of North America and Europe.

The vertical distribution of these plants ranges from the intertidal region to depths of around 60 m (Duarte, 1991; Duarte et al., 2007), and the depth distribution is controlled by a combination of factors including desiccation, wave action, substrate stability, salinity, and light availability (Koch, 2001; Krause-Jensen et al., 2003). The depth distribution of *Z. marina* in a large number of Danish coastal areas reflects a balance between exposure to physical stresses in shallow water and limited light availability in deep water (Fig. 5.3), and these appear to be the most important factors controlling the upper and lower depth limits of these plants (Krause-Jensen et al., 2003).

Along the land−sea axis of estuaries, the abundance and species composition of submersed plant communities generally vary systematically with changes in salinity, along with physical exposure and water clarity. A few species such as the seagrass *Ruppia maritima* occur throughout the salinity range from landward riverine sites to oceanic water at the mouth of an estuary, while most other species have relatively narrow distributions along the estuarine salinity gradient. Typically, water clarity, and hence plant depth penetration, is low at the riverine end of estuaries due to greater nutrient and silt inputs from land but much higher at the oceanic end of the salinity gradient.

5.2 STANDING CROP AND PRODUCTION

Depending on species and latitude, the biomass and production of submersed plants tend to vary
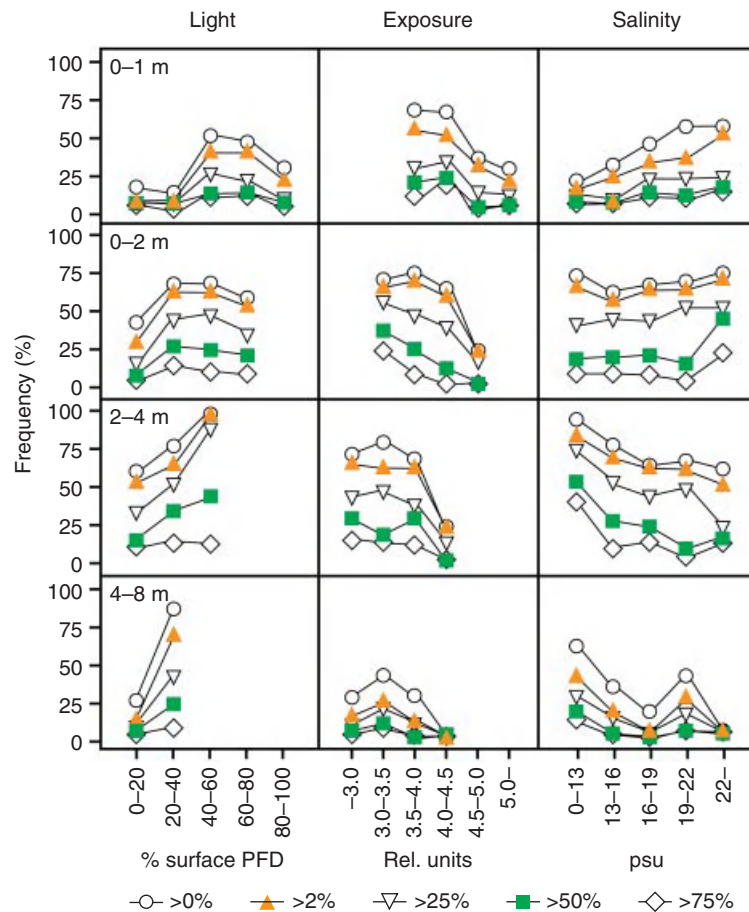
FIGURE 5.3 The probability of finding eelgrass at a cover (in % of bottom area) of greater than 0, greater than 2, greater than 25, greater than 50 and, greater than 75% at different depth intervals and as functions of light availability (in % of surface photon flux density, PFD), wave exposure (in relative units determined by fetch, wind direction and velocity, and water depth; Krause-Jensen et al., 2003) and salinity. *Source:* Redrawn after Krause-Jensen et al. (2003).

considerably on seasonal and annual scales (Fig. 5.4). Temperate freshwater species and intertidal beds of *Z. marina* in the Dutch part of the Wadden Sea are annual species that disappear during winter and grow up from rhizomes or seeds in spring. In subtropical or tropical waters, seagrass biomass may fluctuate very little over the annual cycle, and the clonal plants may have shoots that are interconnected for years, decades, or even centuries (Hemminga and Duarte, 2000). The biomass of freshwater plants growing in brackish and midsalinity areas is typically moderate but occasionally relatively high (e.g., $700–800$ g dw m^{-2}; Gruber and Kemp, 2010). While the standing crop of the small *Halophila* species is generally low, species of the genera *Amphibolis, Phyllospadix*, and *Posidonia* often accumulate very high biomass, exceeding 1000 g dw m^{-2} (Duarte and Chiscano, 1999). As discussed in the next section, dense beds of seagrasses can greatly influence the

conditions in shallow waters by providing food and shelter for invertebrates and fish, damping waves and currents and hence preventing coastal erosion, and by promoting sedimentation of organic and fine particulate matter within the bed.

Seagrass production has been the subject of considerable attention since early in the last century, when Ostenfeld (1908) and Petersen (1918) examined the depth distribution and biomass of *Z. marina* and estimated its importance as a source of organic matter to benthic invertebrates and fishes. It is often suggested that seagrass meadows are among the most productive aquatic ecosystems with annual rates of up to 1000 g C m^{-2} (Mann, 1972; McRoy and McMillan, 1977; Zieman and Wetzel, 1980). These generalizations are supported by comparison of published daily rates of above- and below-ground production of a large number of seagrass species, where aboveground rates generally range between 1 and
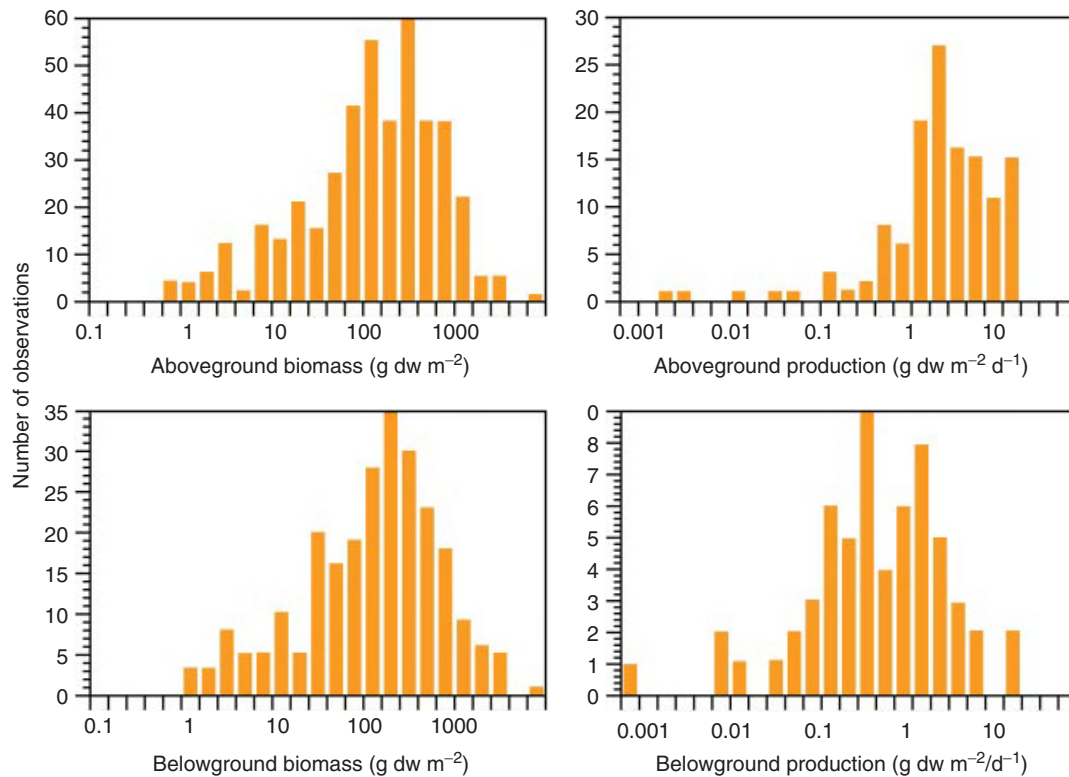
FIGURE 5.4 Frequency distribution of biomass and production compiled for a large number of seagrass species. Redrawn after Duarte and Chiscano (1999).

10 g dw m^{-2} d^{-1} and below-ground rates tend to be lower but still significant (Fig. 5.4; Duarte and Chiscano, 1999). One might expect tropical seagrasses to be the most productive, but the compilation of data across species and studies actually shows that both aboveground biomass and daily production tend to increase with increasing latitude (Duarte and Chiscano, 1999).

5.3 FACTORS REGULATING SUBMERSED VASCULAR PLANTS

The biomass and production of all autotrophs are regulated by many different factors acting alone as ultimate regulating factors or in concert as multiple limitations. Often, when regulating factors are examined, focus is on resource limitation of photosynthesis and growth, but loss factors may be equally important in limiting plant biomass accumulation and hence for areal production. For example, herbivore grazing can remove an associated photosynthetic potential, and under some conditions this may be an important constraining factor (Heck and Valentine,

2006). Physical disturbance through wave actions is another potentially important factor, which can tear leaves and erode whole rooted plants from sediments (Koch, 2001). High physical stress often prevents submersed plant colonization and is the most important factor causing complete absence of submersed plant beds from shallow, physically disturbed waters. This fact seems to have been surprisingly ignored in the estuarine literature on submersed plants.

When dealing with the more traditional factors regulating plant production (e.g., light, inorganic carbon, and nutrients), environmental control of production is often attributed to either light, nutrient, or carbon limitation in accordance with Liebig's "Law of the Minimum" developed for agricultural crops (Liebig, 1863). This law assumes that at any time only one factor is the bottleneck that limits plant growth, ignoring the fact that these factors are highly interrelated. For example, increasing nitrogen contents in plants may improve the light-harvesting capacity through accumulation of higher pigment and enzyme concentrations or may similarly improve the dissolved inorganic carbon (DIC) extraction capacity, thereby partly ameliorating limitation by low light or DIC availability (Beardall et al., 1991). Bearing this in

mind, we present the potentially limiting individual factors below, acknowledging that, although interdependent, a single factor is often most limiting to photosynthesis or growth at any one time.

5.3.1 Light

Irradiance within the wavelength range of 400–700 nm (PAR, photosynthetic active radiation) is the ultimate limiting factor controlling the fixation of inorganic carbon through photosynthetic processes. At the level of the individual leaf, photosynthesis versus irradiance (P–I) follows the same hyperbolic response pattern as it does for microalgae and terrestrial plants. At low irradiance, carbon fixation increases almost linearly with irradiance reflecting the light-harvesting capacity of the photosynthetic apparatus determined by pigment contents. At higher irradiance, carbon fixation does not keep up with irradiance, and at some irradiance level the leaf becomes light saturated (i.e., no change in P with increases in I). Compared to microalgae, light saturation for leaves of submersed plants occurs at relatively higher irradiances (>200 μmol photons m^{-2} s^{-1}) and there is little evidence of light inhibition at high irradiances.

Such P–I curves for submersed vegetation are relevant for physiological studies and comparisons but not for estimates of *in situ* photosynthesis (Binzer and Sand-Jensen, 2002). In the field, light does not reach the leaf surface as a perpendicular beam of photons. Instead, irradiance passes down through the canopy while partly being attenuated, and it hits leaf surfaces from multiple angles often very different from $90°$. Consequently, the P–I curves for well-developed canopies are very different from those of individual leaves, often with no clear saturation irradiances and a continuous increase in integrated photosynthesis even at irradiances exceeding maximum midday levels (Binzer and Sand-Jensen, 2002). Accordingly, dense canopies of submersed plants are always light limited, and any increase in day length or average daily irradiance will increase photosynthesis and production.

The importance of light for seagrass distribution is immediately apparent when comparing seagrass depth penetration for different species with light attenuation at the sites where the plants grow (Fig. 5.5; Duarte, 1991; Duarte et al., 2007). Relatively independent of species, the maximum depth penetration of the plants corresponds to irradiance levels ranging from approximately 10–25% of the surface irradiance. These light levels at the maximum depth, which are often referred to as *the minimum light requirements for seagrasses*, are much higher than those needed by
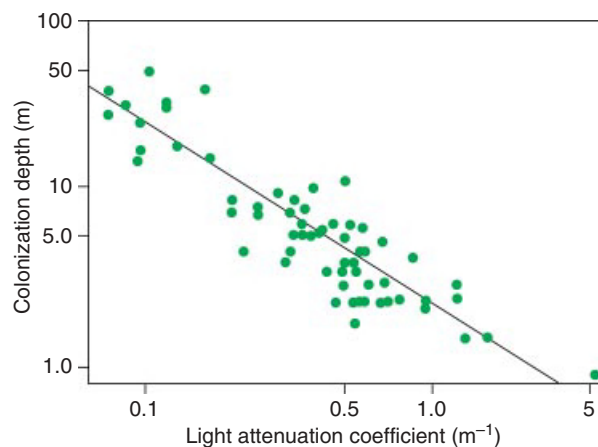
FIGURE 5.5 Colonization depth for seagrass communities distributed worldwide versus light attenuation coefficient reflecting water turbidity. The relationship is described by the equation $\log(Z_c) = 0.26 - 1.07 \cdot \log(k)$, where Z_c is the colonization depth and k is the light attenuation coefficient. Redrawn after Duarte (1991).

micro- and macroalgae, which are typically about 1% of the surface irradiance, but sometimes much lower (e.g., 0.001%, Markager and Sand-Jensen, 1996). The high light requirements of rooted submersed plants might be explained by the energetic costs related to growth and maintenance of below-ground tissues or the need for surplus oxygen transport to roots to oxidize and detoxify reduced metabolites within the sediments (e.g., Kemp et al., 2004). However, these very high minimum light levels required for submersed vascular plants have still not been fully understood (e.g., Zimmerman et al., 1997).

5.3.2 Temperature

Temperature in general exerts strong effects on plant metabolism, physiology, and life cycles. Often, specific stages of the life cycle of the plants, such as flowering or fruit development, occur within much narrower temperature regimes than those required for plant growth (McMillan, 1976). When temperatures become too high, however, they can be deleterious for plant performance in general (Masini and Manning, 1997).

Gross photosynthesis (P_g) of eelgrass increases exponentially with increasing temperature and gradually declines above an optimum temperature level, as photosynthetic enzymes begin to degrade (Staehr and Borum, 2011). Plant respiration (R) also increases with temperature but at a greater rate, and maximum rates of respiration are reached at higher temperatures than those for photosynthesis. Combining these effects of increasing temperature, net photosynthesis ($P_g - R$) increases exponentially
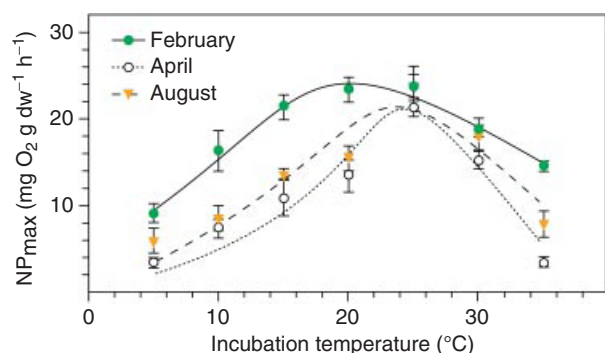
FIGURE 5.6 Temperature dependency of light saturated net photosynthesis for eelgrass collected in winter (February), spring (April), and late summer (August). Optimum temperature for light saturated net photosynthesis varied from 20 to 25°C depending on the season. *Source*: Redrawn after Staehr and Borum (2011).

with moderate increases in temperature, then gradually declines above an optimum temperature level (Fig. 5.6) and may become negative at very high temperatures (Greve et al., 2003). Hence, temperatures of 10–15 °C above the optimum for a certain plant species may cause physiological damage to the tissues and may also result in a negative carbon balance for the plant, giving other plant species an advantage in the competition for space.

5.3.3 Salinity

Salinity is an important factor affecting plant success, as reflected by the changes in species composition of the submersed plant populations along the land–sea axis. The salinity tolerance of plants largely depends on their ability to accumulate organic solutes to maintain turgor pressure. The freshwater species occurring in estuaries tolerate, to varying degrees, moderate salinities, while one seagrass species, *R. maritima* (widgeon grass), has a very wide salinity tolerance (down to zero salinity). When gradually acclimated to increasing salinities, turtlegrass, shoalgrass (*Halodule wrightii*), and widgeongrass are tolerant to salinities as high as 70 psu (twice the salt of seawater), which may occur during periods of low precipitation and high evaporation in shallow lagoons (Koch et al., 2007). Hypersalinity (i.e., levels above that of sea water), however, generally has negative impacts on most seagrass species, severely disturbing their osmoregulatory capacity (Walker and McComb, 1992; Koch et al., 2007). High salinities in Florida Bay, USA, resulting from high evaporation during summer and reduced freshwater discharge through the Everglades due to human interference, are assumed to contribute to widespread seagrass die-offs (Zieman et al., 1999).

5.3.4 Nutrients

All plants need a certain amount of nutrients to satisfy growth requirements. In general, nutrient uptake per biomass is higher for small organisms than for large because the former have a much larger relative surface area across which nutrients are absorbed (Hein et al., 1995). However, larger plants tend to grow more slowly and thus have lower nutrient requirements over time. Plants often have the ability to take up nutrients in excess during periods of low growth, and this excess is then used during periods of high growth. Hence, large slow-growing plants with low ratios of surface area to volume, such as kelps and submersed vascular plants, seem to suffer less from long-term nutrient limitation compared to fast-growing but ephemeral macroalgae and microalgae (Pedersen and Borum, 1996). In addition, the submersed vascular plant roots, which have access to the much richer supplies of nutrients within the sediment porewaters, tend to be less vulnerable to nutrient limitation (Hemminga, 1998).

Although seagrasses take up nutrients from both water column and sediment and in general have relatively low requirements, temporal nutrient limitation of seagrass productivity is often observed. Low levels of sediment ammonium have been reported to be limiting to seagrass productivity (Dennison et al., 1987; Short, 1987; Lee and Dunton, 2000), and, more frequently, phosphorus limitation has been documented for different seagrass species growing in subtropical carbonate sediments, in which most of the phosphorus is tied up in mineral forms not directly available for plant uptake (Short et al., 1990; Fourqurean et al., 1992; Jensen et al., 1998).

5.3.5 Inorganic Carbon

The role of inorganic carbon as a potentially limiting factor for photosynthesis of submersed vascular plants has become an issue of increasing interest due to the rising atmospheric CO_2 level and global climate change. As mentioned in the introduction to this chapter, limited availability of inorganic carbon is potentially a bottleneck to the growth of submersed plants because of their terrestrial origin and their relatively short evolution period for adapting to all challenges of life in the aquatic environment (Madsen and Sand-Jensen, 1991). Seagrasses readily take up CO_2 from the water, but, like most macroalgae and many submersed freshwater plants, they also have the capacity to extract the much higher concentrations of HCO_3^- (<20 μM CO_2 vs 2.2 mM HCO_3^-; Madsen and Sand-Jensen, 1991). The large total pool of DIC in seawater, however, does not seem to be sufficient to
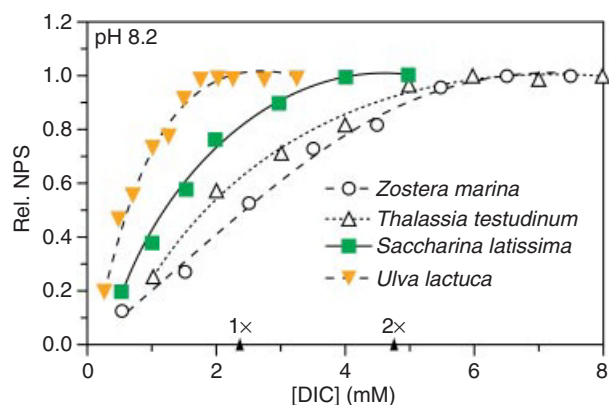
FIGURE 5.7 Net photosynthetic rates relative to maximum net photosynthesis of two macroalgae species: *Ulva lactuca* and *Saccharina latissima* (formerly *Laminaria saccharina*) and two seagrass species: *T. testudinum* and *Z. marina* at normal seawater pH but varying availability of inorganic carbon (DIC in mM). Normal (1×) and double (2×) seawater DIC levels are indicated on the *x*-axis. Redrawn after Beer and Koch (1996).

saturate photosynthesis of seagrasses when examined in single leaf experiments (Fig. 5.7; Beer and Koch, 1996). Accordingly, seagrasses may benefit and gain competitive power relative to macroalgae from rising atmospheric CO_2 levels (Zimmerman et al., 1997). However, one should again be cautious in extrapolating conclusions from single leaf measurements to fully developed plant beds in nature, where many factors, including CO_2 availability, vary simultaneously, which may show high spatial and temporal variability on small scales owing to release from sediments.

5.3.6 Oxygen Dynamics and Sulfide Invasion

The inherent problem faced by submersed plants in supplying roots and rhizomes with sufficient oxygen to support aerobic respiration is not only a physiological challenge (see earlier section), but it is also a potential constraint on plant growth and survival of submersed freshwater plants (e.g., Armstrong, 1979; Dacey, 1980) and seagrasses (Borum et al., 2006). Until recently, it was assumed that the oxygen supply to seagrass roots and rhizomes relied almost exclusively on the oxygen produced by leaf photosynthesis during the day, making roots and rhizomes generally susceptible to anoxia and anaerobic metabolism at night (Smith et al., 1984). This is, however, not the case. At night, when the internal oxygen content of the plant tissues declines below the water column oxygen content, oxygen passively diffuses from the water into the seagrass leaves and is then transported

to rhizomes and roots by gas-phase diffusion through the air-filled lacunae connecting leaves with roots (Pedersen et al., 1998). This transport is inherently rapid (within minutes) because gas-phase diffusion, as mentioned earlier, is about 10^4 times faster than diffusion in water. Under normal circumstances with high water column oxygen, moderate plant respiration and low oxygen consumption in the sediment, the oxygen transport is sufficient to support aerobic root and rhizome metabolism and even sufficient to allow the release of oxygen to the surrounding sediment in the dark (Pedersen et al., 1998; Borum et al., 2006).

The oxygen release to the sediment creates an ''oxic microshield'' around the roots. This shield prevents reduced and often toxic sediment metabolites (e.g., Mn^+, Fe^{2+} or H_2S) from reaching the root surfaces and invading the plant tissue, because the metabolites are rapidly reoxidized by bacteria within the oxic microzone (Lee and Dunton, 2000; Pedersen et al., 2004; Holmer et al., 2005). However, if the roots run low on oxygen, the microshield disappears, allowing metabolites to invade the roots and poison plant tissues (Fig. 5.2). This creates stressful conditions for growth, reducing photosynthesis at low levels and resulting in mortality at higher levels (Holmer and Bondgaard, 2001). These conditions occur if (i) the water column oxygen is low at night, (ii) water mixing is reduced (e.g., Binzer et al., 2005), (iii) plant respiration is high owing to high temperatures or hypersalinity, and/or (iv) the sediment oxygen consumption is accelerated by rapidly degrading organic matter during eutrophication.

5.4 PLANTS AND ECOSYSTEMS

Submersed vascular plants are conspicuous benthic primary producers that have important effects on many ecosystem processes. Their aboveground tissues, which vary in structural complexity with species and environmental conditions, influence water movement, leading to generally quiescent conditions within plant beds. They are also an important part of the food chain, and serve as refuge (from predation) for fish and invertebrates and as substratum for epiphytic colonization. In addition, below-ground, root, and rhizome networks influence sediment biogeochemistry. Submersed plants therefore substantially modify their local environment, producing many positive feedbacks that can increase the suitability of an area for further plant growth as well as negative

feedbacks that can retard plant production (e.g., Jones et al., 1997; Gruber and Kemp, 2010).

5.4.1 Consequences of Physical Effects on Water Movement

Increased frictional drag associated with the physical structure of plant canopies can reduce water velocity (Gambi et al., 1990) and wave heights (Fonseca and Cahalan, 1992) within the plant bed. These effects generally enhance the deposition of fine organic and inorganic particles as velocities drop below a critical threshold (Palmer et al., 2004). In healthy plant beds, particle trapping can elevate the sediment surface relative to that outside the bed (Bos et al., 2007). Suspended particles also directly adhere to seagrass blades (Agawin and Duarte, 2002), trapping them within the plant bed. Quiescent conditions in submersed plant communities can result in substantially longer water residence times compared to unvegetated areas (Rybicki et al., 1997). This has important implications for particle accumulation and dissolved nutrient chemistry. The influence of plant beds on local hydrodynamics and sedimentology depends on key characteristics of the plant canopy including shoot density, shoot length, and aboveground biomass (Fig. 5.8), which vary with species and over space and time (e.g., Hasegawa et al., 2008). Additionally, submersed plants are phenotypically plastic and can acclimate to a range of hydrodynamic conditions, with leaves, for example, minimizing drag by becoming shorter and thinner under higher flow conditions (Peralta et al., 2005).

In addition to trapping particles, submersed plants tend to stabilize the sediment surface through sheltering by leaves and binding by roots and rhizomes. Resuspension of fine sediments is reduced within plant beds even during storm events (Gacia and Duarte, 2001; Granata et al., 2001). As a result, water clarity in plant communities increases (Moore, 2004), thereby increasing the available light for photosynthesis. This effect can be dramatic (e.g., ~50% decrease in turbidity) for dense beds of healthy plants (Fig. 5.9; Gruber et al., 2011). The extent to which this occurs depends on canopy architecture, the nature of the suspended material, and ambient hydrodynamics (Vermaat et al., 2000). Although greater light availability improves submersed plant growth, extreme accumulations of leaf tissues can limit plant growth by self-shading (Marba and Duarte, 2003; McKone, 2009).

5.4.2 Biogeochemical Effects

On local scales, the damping of current and wave energy by submersed plant beds tends to result in

$$y = e^{-0.006x + 0.43}$$
$$r^2 = 0.748*$$
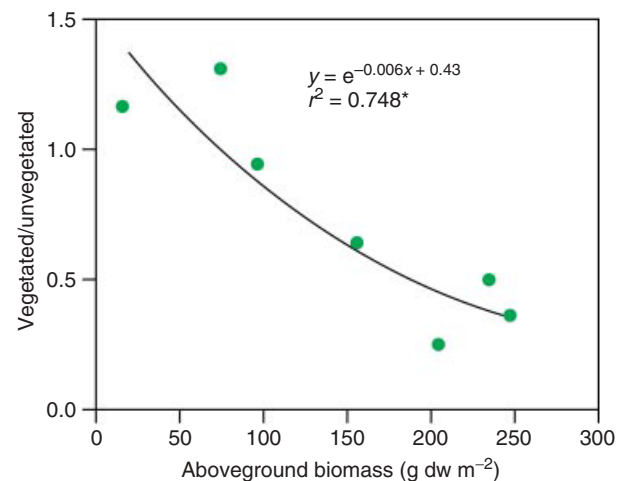
FIGURE 5.8 Ratio between current velocity measured inside and outside an eelgrass bed during periods with different aboveground biomass. The ratio between current velocities clearly declined with increasing biomass, reflecting the damping effect of the canopy. Redrawn after Hasegawa et al. (2008).

accumulation of organic-rich material within vegetated sediments. The decomposition of this trapped organic material augments inorganic nutrient pools, especially in the sediment porewater (Kenworthy et al., 1982; Fig. 5.10). These high nutrient concentrations tend to stimulate plant uptake (e.g., Caffrey and Kemp, 1990). In addition, changes in sediment composition and lower water flow rates favor reduced flushing and mixing of this porewater with the overlying water column (Koch, 1999). Uptake rates of water column dissolved nutrients are strongly influenced by local hydrodynamics, where low current speeds and turbulence retard uptake by epiphytic algae as well as seagrass across respective diffusive boundary layers (Morris et al., 2008). Generally, under oligotrophic and low energy conditions, sediment porewater serves as an important nutrient source for plants.

Interactions between plant roots and sediments also have substantial effects on other important sediment biogeochemical processes. As mentioned previously, radial release of oxygen by roots occurs in submersed plant beds as a function of plant photosynthesis (Kemp and Murray, 1986; Pedersen et al., 1998). Oxygen release into anoxic sediment allows reduced metabolites to be reoxidized. These oxidized microzones around roots can stimulate coupled nitrification–denitrification (Caffrey and Kemp, 1990), as ammonium from the large sediment pool is reoxidized and nitrate then diffuses to the anoxic zone where denitrification occurs. Plant stimulation
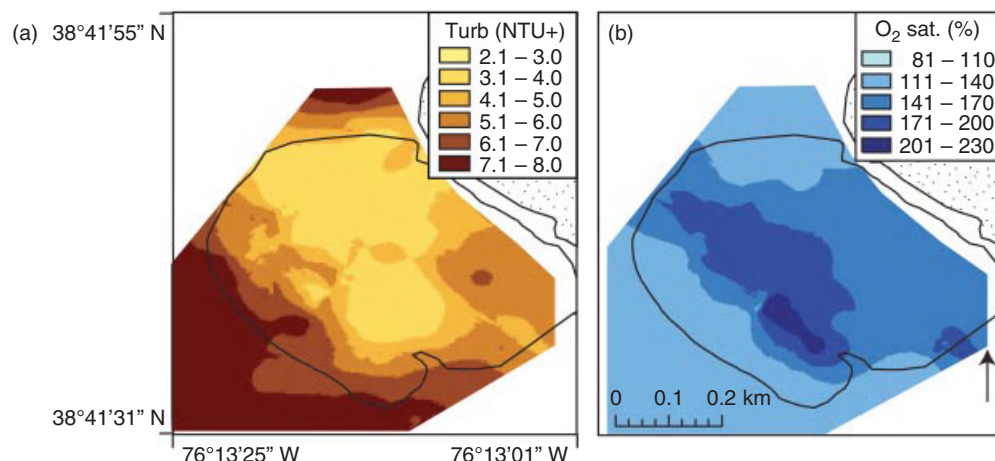
FIGURE 5.9 Maps of (a) turbidity and (b) oxygen saturation created from measurements across and outside a robust bed of *S. pectinata* (sago pondweed) in Chesapeake Bay. The solid black line represents the perimeter of the bed, while the dotted area represents land. Turbidity was measured in NTUs (nephalometric turbidity units), a relative measure of underwater light transmission. The maps show a reduction in turbidity and increase in oxygen saturation with distance into the plant stand, which reflects the substantial impact submersed plant beds can have on water quality in shallow environments. *Source*: Redrawn after Gruber and Kemp (2011).
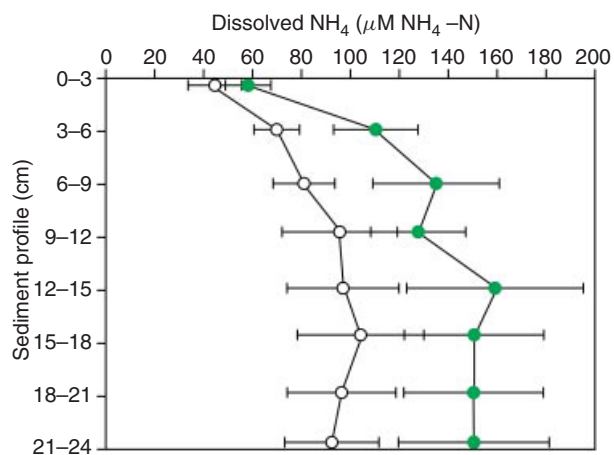
FIGURE 5.10 Sediment profiles of dissolved ammonium in vegetated sites consisting of mixtures of *Z. marina* and *H. wrightii* (closed circles) and unvegetated sites (open circles). Error bars are the standard error. The higher level of porewater ammonium in the seagrass bed reflects the retention and recycling of organic matter produced by the community or trapped from sources outside the plant bed. *Source*: Redrawn after Kenworthy et al. (1982).

of nitrification and denitrification may be substantial for some submersed plants including freshwater isoetids (Christensen and Sørensen, 1986; Ottosen et al., 1999). In some instances, however, denitrification stimulated in seagrass beds may not exceed rates of nitrogen fixation (Risgaard-Petersen and Ottosen, 2000; Rysgaard et al., 1996). Accordingly, the overall impact of submersed plants on nitrogen cycling

appears to vary among species and specific coastal sites.

5.4.3 Submersed Plants as Food and Habitat

Historically it was believed that relatively few organisms grazed directly on submersed vascular plants, and herbivory was of minor importance for seagrass biomass and production (den Hartog, 1970). However, many recent studies have shown the important direct and indirect roles that grazing plays, especially in estuarine plant communities (Heck and Valentine, 2006; Valentine and Heck, 1999). Marine mammals such as dugongs and manatees can gorge on beds of seagrass, leaving long grazing tracks devoid of vegetation (Thayer et al., 1984), and sea turtles, fishes, and urchins can remove up to 50% of leaf production (Cebrian and Duarte, 1998). In estuaries, waterfowl including geese, swans, and diving ducks show a distinct proclivity for submersed plant beds (Holm and Clausen, 2006; Rybicki and Landwehr, 2007), and their grazing represents a major link in estuarine food webs (Weisner et al., 1997). Consequently, reductions in size and density of submersed plant beds owing to human and natural disturbances have been shown to result in large declines in abundance of herbivorous ducks during fall migration periods (Fig. 5.11; Kemp et al., 1984). Research using stable isotopes of carbon and nitrogen suggests that submersed plant primary production supports growth of animals at higher trophic levels, where, for example, in one study half
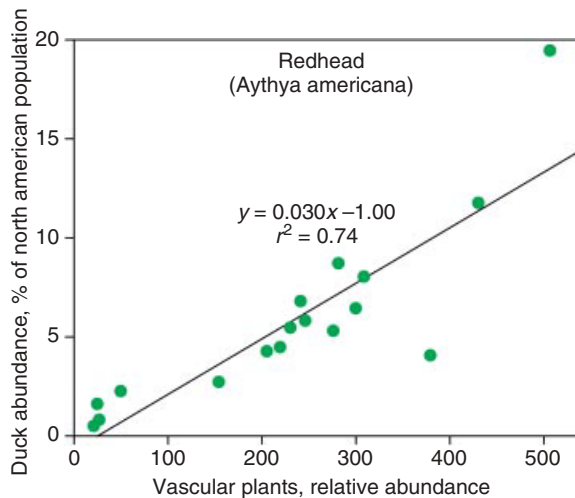
FIGURE 5.11 The abundance of the diving duck, Redhead (in % of the total count for North American breeding grounds), resting during winter in upper Chesapeake Bay versus the relative abundance of submersed vascular plants at upper Bay sites. The number of resting Redheads correlated well with plant abundance during the period from 1961 to 1975. With gradually decreasing plant abundance up through the 1960s and 1970s, Redhead abundance declined in this area and the ducks moved to areas with eelgrass further south in Chesapeake Bay. *Source*: Redrawn after Kemp et al. (1984).

the fauna in a tropical marine ecosystem appeared to depend directly or indirectly on these plants (Vonk et al., 2008).

Additionally, primary production by epiphytic algae on submersed plant leaf surfaces can be at least as large as production by the host plants themselves (Borum et al., 1984). The growth form of most seagrass species is characterized by continuous production of new, clean leaves that replace older leaves, which are often covered with heavy epiphyte growth. Thus, these species tend to maintain a balanced mixture of new, mature, and old leaves with an associated gradient of epiphyte accumulations. Epiphytic algae are a key food source for numerous gastropods, amphipods, isopods, and fish, which leave distinct grazing tracks within the attached community (Jernakoff et al., 1996) and often show a preference for older leaves with dense coatings of epiphytes (Wressnig and Booth, 2007).

Although not as well-studied as many other aspects of submersed plant ecology, the production of dead (detrital) leaf material represents a significant source of nutrients for the wider estuarine community. Detritus is grazed directly by some amphipod species, which ingest not only dead plant material but also its associated epiphytic community (Lepoint

et al., 2006). Leaf material breaks down at widely varying rates, with the total degradation time ranging from less than 80 days (for the proportion that remains in the plant bed) to greater than 370 days for ''wrack'' deposited on beaches (Oldham et al., 2010).

The abundance of organic matter and the protection offered by the submersed plant canopy make these plant beds attractive habitats for many animals. Beds support substantially higher abundance, diversity, and production of fish and invertebrates compared to nearby unvegetated sites (Fig. 5.12; Kemp et al., 1984; Lubbers et al., 1990; Lee et al., 2001). However, few faunal species are completely restricted to seagrass beds (e.g., the fan mussel, *Pinna nobilis*, in Mediterranean *Posidonia* stands) with most species also occurring outside the beds. Some animal species use seagrass beds only during juvenile stages, but a number of species feed and remain within the beds throughout their life cycle (Gillanders, 2006). For fish, submersed plant beds can serve as refuges for predator avoidance (e.g., Canion and Heck, 2009) or can simply be the preferred productive habitat irrespective of predation pressure (Burfeind et al., 2009). Often, submersed plants and fauna have a mutualistic relationship, where for example increased abundance of ribbed mussels in seagrass beds stimulates plant
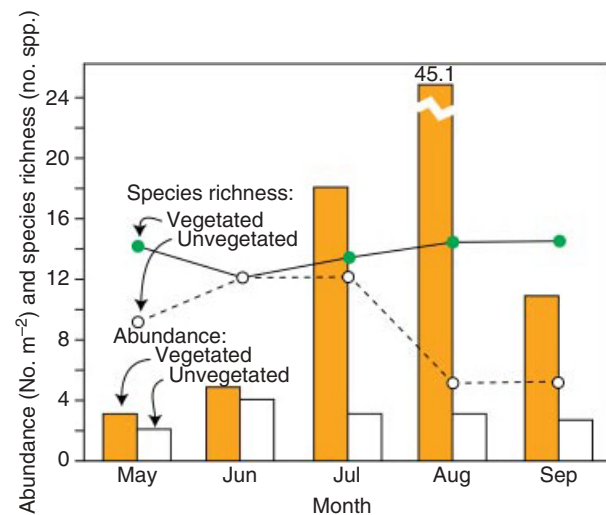
FIGURE 5.12 Abundance (number of individuals per meter square) and species richness (number of species) of finfish from May through September at an unvegetated and a vegetated site in the Choptank River, Chesapeake Bay. In the vegetated area, finfish were more abundant and more species were found compared to those in the unvegetated area, especially in August and September. Redrawn after Kemp et al. (1984).

growth through efficient nutrient recycling (Peterson and Heck, 2001). Plants have also been shown to benefit from epiphyte grazers that increase light availability to leaves, and from sediment infauna that can significantly decrease concentrations of toxic hydrogen sulfide while increasing dissolved nutrient pools (Reynolds et al., 2007).

5.5 SUBMERSED AQUATIC PLANTS AND HUMANS

Submersed plant beds provide many key "ecosystem services" that benefit humans in estuaries and coastal systems worldwide. As mentioned above, their physical structure damps wave energy, which can reduce coastal erosion. This has been observed in many instances. For example, increased shore erosion appeared in Danish coastal waters following the massive die-off of eelgrass (*Z. marina*) populations in the 1930s (Rasmussen, 1973; Christiansen et al., 1981). Submersed plant beds also provide food and habitat for commercially and recreationally important fish and invertebrates. They act as a reservoir of nutrients, potentially suppressing excessive phytoplankton growth and improving water clarity. For example, estimates of submersed plant abundance at historical levels in the Chesapeake Bay, USA indicate that these communities could attenuate nearly half of all present nitrogen inputs to the estuary (Kemp et al., 2005). Similar estimates have been developed for the effect of plant beds on regional budgets for fluxes of suspended sediments, organic carbon, and total nitrogen (Kemp et al., 1984). Quantification of the monetary value of "ecosystem services" provided by seagrass beds worldwide has shown them to be one of the most valuable (per hectare) natural aquatic communities (Costanza et al., 1997). However, it should be stressed that the monetary value of the services provided by seagrasses (e.g., shore protection) is highly variable due to the variability in space and time of the seagrass beds (Koch et al., 2009).

The growing human population and its steadily increasing exploitation of space and natural resources in coastal regions worldwide result in continuous pressure on estuarine and coastal ecosystems. This trend has resulted in a wide variety of stresses on submersed plant communities, such as excessive nutrient enrichment (eutrophication), inputs of toxic contaminants, siltation, coastal construction and physical disturbance by dredging, as well as human recreational and fisheries activities (Orth et al., 2006). In addition, climate change is predicted to have a number of negative effects on seagrass ecosystems related to rising temperatures, increasing runoff of nutrients with greater precipitation, higher frequency and strength of storm events, and rising sea level (Short and Neckles, 1999; Najjar et al., 2010). Deterioration of seagrass beds has been observed over wide geographical scales (Waycott et al., 2009; Duarte, 2002). In fact, it has been estimated that nearly 30% of worldwide seagrass area has been lost since the 1870s and that the rate of loss continues to increase (Fig. 5.13).

The loss of submersed plant beds has resulted in increased attention by estuarine resource managers who have implemented monitoring programs that track changes in bed cover and density of submersed plants to detect and mitigate negative trends in abundance of these valuable living resources (Orth et al., 2002, 2010a). The process of mapping existing plant beds has evolved over the last century from labor-intensive sampling of plants along depth gradients to present surveys that apply acoustic instruments, high resolution aerial photography, and satellite imagery techniques (Orth et al., 2010b); this is much easier for researchers today than it was for the early Danish seagrass researchers (e.g., Ostenfeld, 1908). Considerable effort has also gone into establishing habitat quality thresholds for submersed plants, which aim to define minimum light requirements or maximum nutrient levels needed to restore and protect submersed plant beds (Dennison et al., 1993; Kemp et al., 2004). These can be used in simulation models to predict plant response to alternative restoration and mitigation efforts (e.g., Madden and Kemp, 1996; Cerco and Moore, 2001; Latimer and Rego, 2010).

As submersed plants are now absent from many areas where they historically grew, reintroduction often becomes part of an estuary management plan, and many techniques are available (Fonseca et al., 1998). Of course, selecting the most appropriate restoration method requires information on the life history of the particular plant species. For some seagrasses, such as the Mediterranean *P. oceanica*, growth occurs slowly through rhizome extension, and natural recovery even in small, denuded areas (e.g., 10 m^2) may take decades (Hemminga and Duarte, 2000). For other species with multiple reproduction strategies, an improvement in water clarity through reductions in nutrient and sediment loads may be sufficient for natural reestablishment. Mixed success has, however, been achieved using various seeding and planting techniques (Orth et al., 2010b).
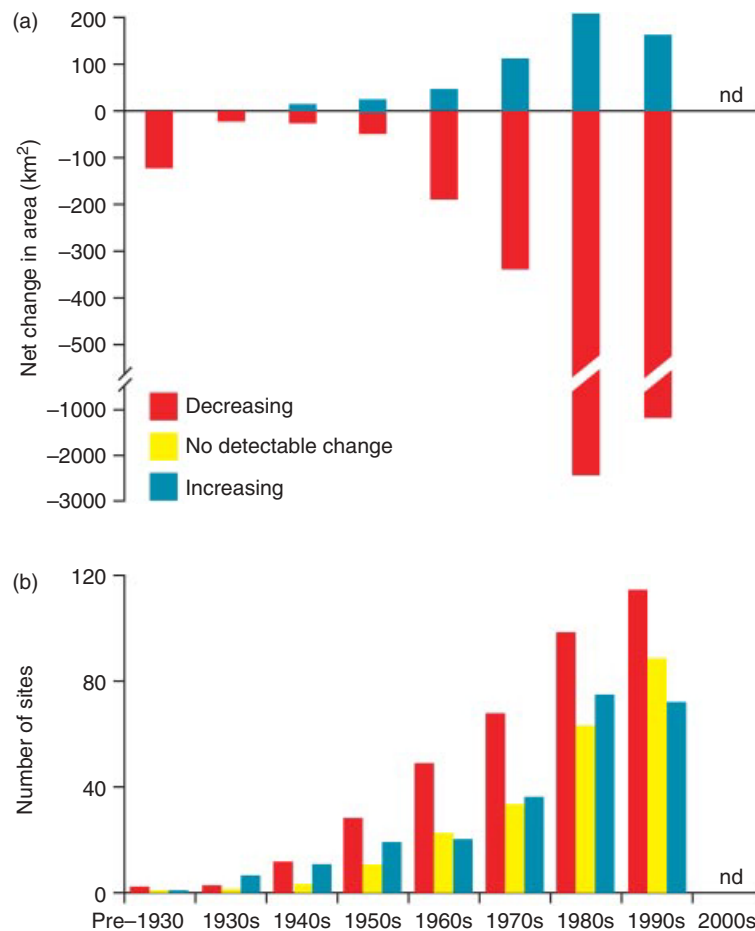
FIGURE 5.13 Decadal trends in gains and losses of seagrass beds recorded world wide. (a) Decadal gains and losses of area covered by seagrass and (b) number of sites where changes (decreasing, increasing, or no change) have been recorded. The records show higher areal losses relative to gains and a relatively larger number of sites exhibiting decreases than increases of seagrass area since the 1950s. Redrawn after Waycott et al. (2009).

As mentioned previously, a complex network of interactions exists between submersed plants, hydrodynamics, sediments, and associated organisms, which can result in positive feedback effects on plant growth. Restoration ecology is beginning to incorporate some of these concepts in a practical way (Byers et al., 2006), including optimization of site choice (Hengst et al., 2010; van Katwijk et al., 2009), planting density (van der Heide et al., 2007), and transplant types and sizes (Bouma et al., 2009). In addition, it has been proposed that the effectiveness of submersed plant restoration efforts would be greatly enhanced by incorporation of the self-catalyzing positive feedback effects of these beds into the design of revegetation programs (van Katwijk et al., 2009; Kemp et al., 2005). The application of these theoretical concepts to real-world systems is in its infancy, and a great deal of room remains for improvements in submersed plant management and restoration techniques.

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CHAPTER SIX

COASTAL MARSHES

Carles Ibáñez, James T. Morris, Irving A. Mendelssohn, and John W. Day Jr.

6.1 INTRODUCTION

Coastal marshes with emergent vegetation are a common feature of most estuaries and coastal plains all over the world. Salt marshes are the most abundant wetland type, but brackish and freshwater marshes are also present in many estuarine systems (Day et al., 1989). Coastal marshes are beds of intertidal rooted vegetation that are alternately inundated and drained by the tides. Marshes occur principally along temperate and boreal coasts (Fig. 6.1) but often form in the tropics on salt flats not occupied by mangroves. There is an almost constant interaction between water and marsh. This is facilitated by a complex network of channels through which water, suspended and dissolved material, and organisms pass. Grasses are normally the dominant primary producer, although sometimes low, shrubby vegetation replaces grasses. In addition, many types of algae grow on the plants and on the surface of the mud. Coastal wetlands are generally composed of either salt marshes or mangrove swamps. The mangrove community occurs along tropical shores and is made up of trees, while coastal marshes are grass communities found principally in the temperate zone. The two communities are ecologically analogous because of their physical location, ecological processes, and trophic contribution to the overall estuarine ecosystem. Mangroves are the subject of Chapter 7, so here we focus on marshes.

Numerous studies of coastal marshes show that they are among the most productive plant communities in the world and are often a large proportion of the total area of estuaries. Coastal wetlands also play important functions and values in terms of ecosystem services, from which humankind benefits. In this chapter, we discuss the structure, composition, distribution, productivity, functions, assessment, and human impacts of coastal marshes and the factors that affect productivity. There is an abundant literature about the ecology of coastal marshes, especially of salt marshes, mostly produced over the last 40 years (Teal, 1962; Redfield, 1965, 1972; Nixon and Oviatt, 1973; Odum, 1974, 1980, 1988; Chapman, 1977; Kirby and Gosselink, 1976; Zedler, 1977; Valiela and Teal, 1979; Howarth and Teal, 1980; Gallagher et al., 1980; Pomeroy and Wiegert, 1981; Mendelssohn et al., 1981; Dijkema, 1987; Adam, 1990; Bertness, 1992; Pennings and Callaway, 1992; Bertness and Shumway, 1993; Teal and Howes, 1996; Kwak and Zedler, 1997; Baldwin and Mendelssohn, 1998; Chambers et al., 1998; Gough and Grace, 1998, 1999; Craft et al., 1999; Hacker and Bertness, 1999; Weinstein and Kreeger, 2000; Mitsch and Gosselink, 2001; Emery et al., 2001; La Peyre et al., 2001; Silliman et al., 2005; Deegan et al., 2007; Sullivan et al., 2007; van Wesenbeeck et al., 2008).
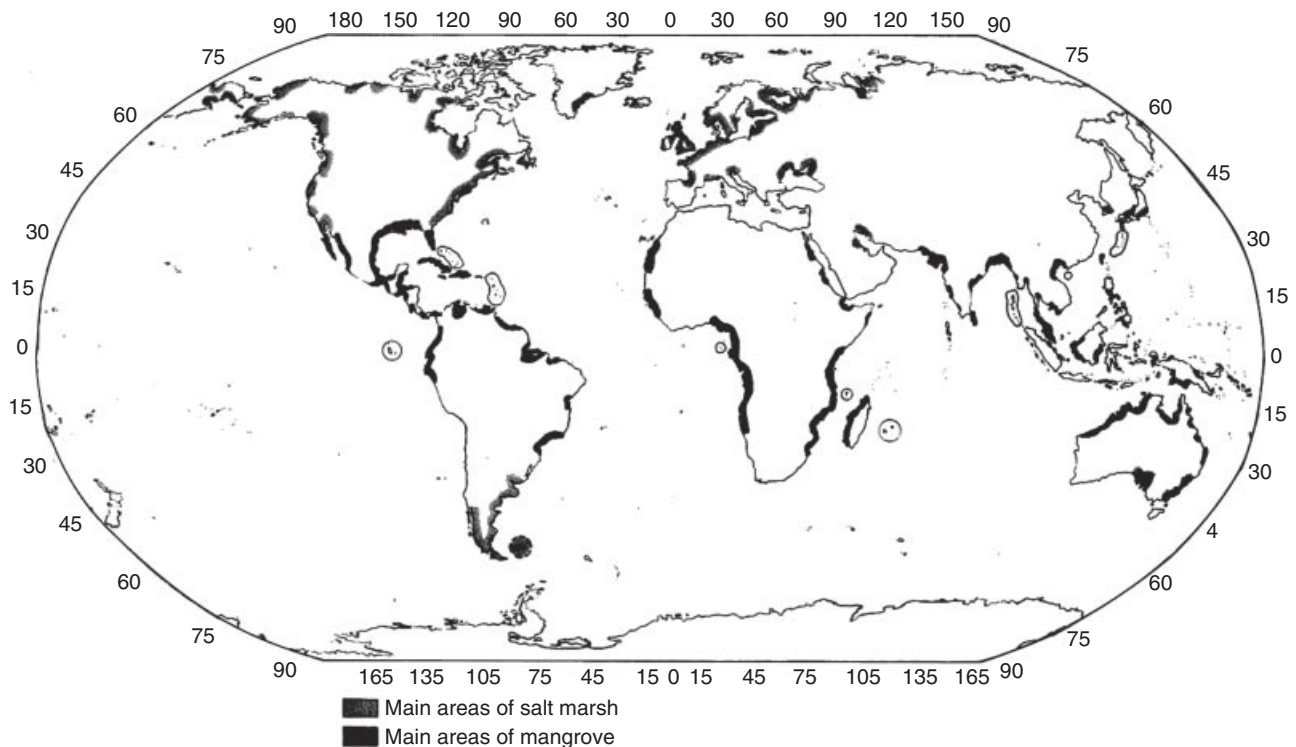
FIGURE 6.1 Worldwide distribution of coastal marshes and mangrove swamps. *Source*: After Chapman (1960).

6.2 GENERAL FEATURES AND TYPOLOGY OF COASTAL MARSHES

The appearance of salt marshes differs along different coasts. Along the southeastern and Gulf of Mexico coasts of the United States, for example, marshes are often dense and robust. By contrast, high latitude coastal areas generally support short, sparse stands of marsh. In an attempt to explain this variability, Chapman (1960) divided salt marshes into nine broad groups based on physiognomy, floristic composition, and geographic distribution (Table 6.1). He also listed over 600 species of plants that grow in salt marshes throughout the world. Species diversity is lowest in the arctic and generally increases toward lower latitudes. A number of genera are broadly distributed and are major components of the flora in many areas (Fig. 6.2). *Puccinellia* is common along northern coasts where ice and extremely low temperatures occur in winter. *Spartina, Juncus*, and *Distichis* are common along nonrocky temperate coasts of Europe, Asia, and North and South America. *Limonium* is found along rugged coasts. *Salicornia*

and related species have the broadest distribution; they are found in microtidal marshes and in the upper intertidal zone in practically all areas because of their ability to withstand desiccation and salinity stress.

The most extensive development of coastal marshes occurs in areas of low relief, abundant rainfall, muddy to sandy coasts, and moderate climate. In the United States, the broadest development occurs along the east coast of the north Atlantic and the Gulf of Mexico. Here, there is sufficient rainfall evenly spread through the year, gentle coastal slopes, and muddy to sandy sediments. The largest single area of coastal marshes is in the delta of the Mississippi River, where almost 40% of coastal salt marshes ($\sim 2 \times 10^6$ ha) of the contiguous United States occur. Extensive wetlands are found in deltas worldwide.

To understand the factors affecting the distribution and features of marsh types, it is important to contrast the differences between tidal and nontidal (microtidal) coastal systems (Table 6.2). Tidal systems are widespread and abundant in most of oceanic coasts, whereas microtidal systems are restricted to semienclosed seas, such as the Mediterranean, Black

TABLE 6.1 Worldwide classification of salt marshes based on geographic distribution, floristic composition, and physiognomy

Group	Geographic Distribution	Dominant Plants	Important Controlling Parameters
Arctic	Greenland, Iceland, and arctic coasts of North America, Scandinavia, and Russia	*Puccinellia phryganodes Carex sp.*	Ice, extreme low temperature
Northern Europe	Iberian peninsula north to Norway and southwestern Sweden West coast of Great Britain, Scandinavia Coasts of Baltic Sea Along English Channel and other muddy coasts	*Puccinelia maritime, Juncus gerardii, Salicornia* spp., *Spartina* spp., *Festuca rubra, Agrostis stolonifera, Carex palecea, Juncus bufonius, Desmoschoenus bottnica, Scirpus* sp., and *Spartina townsendii*	Sufficient precipitation Sandy to muddy substrate Modeate climate Coast with a high proportion of sand Low to moderate salinity Muddy coasts
Mediterranean	Along Mediterranean coasts	Much low shrubby vegetation, *Arthrocnemum, Limonium*, *Juncus* and *Salicornia* spp.	Arid to semiarid, Rocky to sandy coasts Generally high salinity Moderate temperatures
Eastern North America	Temperate Atlantic and Gulf of Mexico coasts of North America	*Spartina alterniflora, Spartina patens, Juncus roemerianus, Distichlis spicata, Salicornia* spp., *Puccinellia maritima* at higher latitudes	Generally muddy coasts and moderate climate Broad development of marshes
Western North America	Temperate Pacific coasts of North America	*Spartina gracilis, Spartina foliosa, Frankenia* spp., *Salicornia* spp.	Arid in south to high precipitation in north Rugged coasts Limited marsh development
Sino-Japanese	Temperate Pacific coasts of China, Japan, Russia, and Korea	*Triglochin martima, Limonium japonicum*; also *Zoysia macrostachya, Salcornia* spp.	Rugged, Uplifting coasts Limited marsh development Moderate precipitation
South America	South America coasts too cold for mangroves	Unique species of *Spartina, Limonium, Dstichlis, Juncus, Heterostachys* and *Allenrolfea*; also *Salicornia* spp.	Rugged coasts Geographic isolation
Australia	South Australia, New Zealand, and Tasmania	*Hemichroa* spp., *Arthrocnemetum* spp., and *Salcornia* spp.	
Tropical	Saline flats not occupied by mangroves	*Salicornia* spp., *Limonium* spp., and *Spartina brasiliensis*	Rainfall Geographic isolation High salinity

Source: After Chapman, 1960. Note scientific names are those used by Chapman.

and Baltic Seas, and the Gulf of Mexico. A major portion of microtidal coastal wetlands are located in deltaic areas, which in many ways have opposite features to classical estuaries. Deltas protrude into the sea and their estuaries are river dominated, whereas typical estuaries are coastal indentations more dominated by tides. Tidal marshes often occur in coastal plain estuaries and along the shores of bays, where there is both tidal activity and riverine influence, leading to close coupling between wetlands and adjacent water bodies. In nontidal areas of coasts, marshes are either not directly connected to estuaries but are frequently associated with coastal lagoons, or they are located in the upper reaches of estuarine systems beyond tidal influence. Tidal marshes occupy large areas often associated with coastal plain estuaries and are characterized by strong and regular tidal fluxes, which play a crucial role in ecosystem functioning. Microtidal river mouths are typically salt-wedge estuaries that are part of a delta (Ibáñez
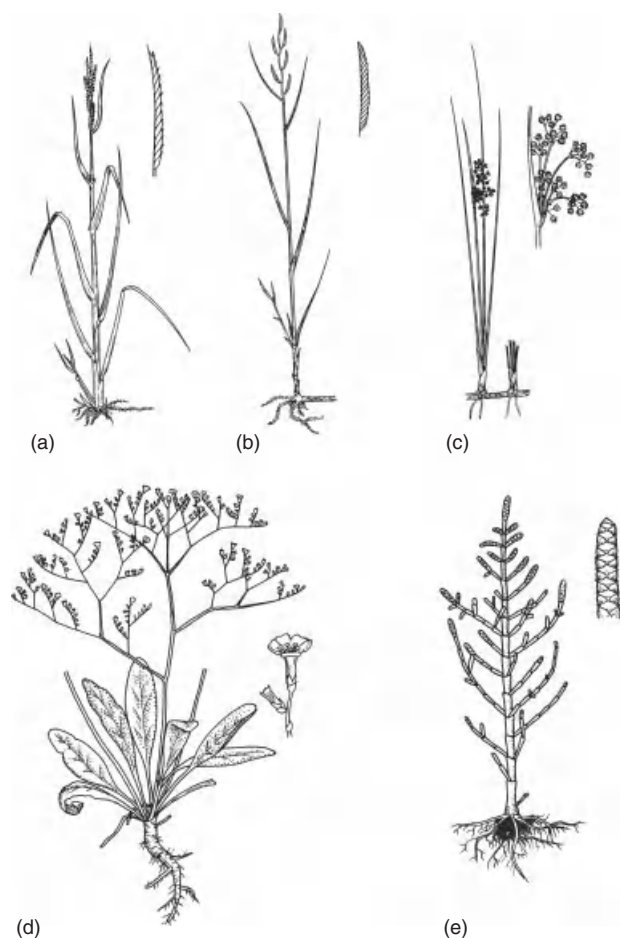
FIGURE 6.2 Several common species of salt marsh plants. (a) *Spartina alterniflora*, (b) *Spartina patens*, (c) *Juncus roemarinus*, (d) *Limonium carolinianum*, and (e) *Salicornia bigelovii*.

et al., 1997a), and the role of the weak tide in the ecosystem is less relevant. Sea level changes due to seasonal cycles and storms likely play a more important role than astronomical tides in microtidal marshes.

Natural levees are the highest parts of deltas and, under natural conditions, are vegetated by riparian forests, which are flooded only during high discharge. In contrast, tidal marshes are located along the shores of the estuarine portion of deltas, which often have a typical valley-shaped topography. In both cases, fresh, brackish, or saline marshes, depending on factors such as elevation, inputs of upland runoff, riverine and tidal influence, and soil drainage often occur. In most cases, there is a clear vegetation zonation mainly related to soil salinity and flooding regime, which is discussed in the following section.

6.3 DISTRIBUTION AND ZONATION OF COASTAL MARSHES

Observations of tidal wetlands in many different areas of the world reveal similar spatial patterns of distribution of plants. Often, the distribution takes the form of bands or zones of different assemblages of plants that are similar from one location to another. Such zonation provides insight into how different plants deal with and alter environmental gradients of the intertidal zone. In this section, we describe distribution and zonation of marsh plants in estuaries and discuss the factors responsible for this structure.

Distribution and zonation patterns occur at several different spatial scales. At the broadest level, there are *latitudinal patterns* where climate plays a major role in affecting marsh distribution. At an intermediate scale, there are *drainage basin patterns*, where water salinity and coastal morphology are important in determining zonation. Finally, *local patterns* occur along and across estuaries as a result of elevation changes and variation in tidal water exchanges as one moves closer to, or further from, a tidal creek. In addition, some worldwide distribution patterns occur as a result of geographic isolation (e.g., the unique vegetation assemblages of Australian and South American salt marshes). Also, in all wetlands, there is local "patchiness" caused by adjustment of plants to various types of small-scale heterogeneity. Bertness and Pennings (2000) suggested that our current understanding of marsh zonation patterns is oversimplified and that the processes creating these patterns may vary in importance between marshes. We now consider distribution and zonation at these spatial scales (latitudinal, drainage basin, and local) in more detail.

6.3.1 Latitudinal Patterns

On a broad latitudinal scale, distribution of coastal marshes in the northern hemisphere is affected primarily by climate (Day et al., 1989). As indicated earlier, mangroves grow in the tropics and temperate regions to about 30 °N. Marshes are present along north temperate coasts from about 30 °N up to 65 °N latitude. Above this latitude, ice and extremes of temperature prevent marsh formation. On the Atlantic coast of North America, there is no aboveground winter biomass higher than about 38 °N latitude due to ice scour (Turner, 1976).

TABLE 6.2 Some differences between tidal temperate and nontidal (microtidal) temperate estuarine systems

Tidal Estuarine Systems	Microtidal Estuarine Systems
Tidal range 1–10 m	Tidal range 0.1–1 m
Astronomical tides > meteorological tides	Astronomical tides < meteorological tides
Tide-dominated estuaries	River-dominated estuaries
Coastal plain estuaries	Deltas, coastal lagoons
Partially and well-mixed estuaries	Salt-wedge estuaries
Extensive tidal marshes	Often small and localized microtidal marshes
Presence of tidal freshwater marshes	Microtidal freshwater marshes rare
Marshes located along the shore of the estuary	Marshes located along coastal lagoons and outer coast
Marshes with regular flooding	Marshes with summer drought and salt stress; irregular flooding
High biological productivity	Often marshes with medium to low biological productivity
Maximum productivity usually from high to middle marsh	Maximum productivity usually from low to middle marsh
Marsh diversity gradient along the estuary	Marsh diversity gradient across the river delta
Plant zonation mainly due to tidal flooding	Plant zonation mainly due to maximum summer salinity
Higher topographic gradient, lower habitat patchiness, and tidal creeks	Lower topographic gradient, higher habitat patchiness, and little tidal creeks

Climate may have important, but largely unrecognized, effects on marsh plant community organization. In cool temperate marshes, low soil salinities result in salinity playing only a minor role in maintaining marsh plant distributional patterns. In contrast, at lower latitudes, hotter climates lead to salt accumulation, elevated soil salinities, and marsh zonation patterns that are strongly driven by soil salinity patterns (Bertness and Pennings, 2000).

Within this general temperature gradient, rainfall plays an important role. Where seasonal moisture deficits exist in tidally flooded land, barren flats may exist in emergent wetlands. Under conditions of extreme or prolonged dryness, there may be little or no vegetation in the intertidal zone. These points are illustrated by patterns of wetland distribution around the Gulf of Mexico, which extends from the tropics in the south to the temperate zone in the north and includes a large variation in temperature and rainfall (Fig. 6.3). Annual rainfall exceeds 1500 mm along the north central and southern coasts. Arid areas with less than 1000 mm occur on the northwestern Yucatán Peninsula near Progreso and in the western Gulf between Tampico and Galveston. These temperature and rainfall gradients affect the distribution of coastal vegetation. Mangroves occur along the tropical and semitropical coasts south of Cedar Keys in Florida and generally south of Port Isabel, Texas. With the exception of a few isolated stands of black mangrove in the Mississippi deltaic plain, mangroves are absent from the northern Gulf Coast, which is dominated by salt marshes. This is changing,

however, due to recently warmer temperatures, possibly a result of climate change (Chapter 20).

In high rainfall areas, intertidal wetlands tend to cover the entire tidal plain. Thus, the Gulf areas with the broadest development of intertidal vegetation are the marshes of the Mississippi River deltaic plain and the mangrove swamps surrounding the Laguna de Terminos and in the delta of the Grijalva River. In the arid areas, marsh vegetation generally occurs only on the more frequently flooded parts of the intertidal zone. The higher parts of the tidal plain are barrens devoid of higher plant life. Halophytes such as *Salicornia* often grow in a narrow zone between the barrens and wetland vegetation growing in the lower tidal plain.

6.3.2 Drainage Basin Patterns

If we travel landward from the barrier stand shoreline, for most estuaries, there is a progressively diminishing tidal influence until at some point there is no longer a tide. Within this area affected by the tide, there is generally also a salinity gradient. Obviously, near the sea the mean salinity is near that of seawater. As seawater mixes with freshwater, the salinity decreases moving inland, until a point is reached where there is always freshwater. Tidal and salinity dynamics are complex, and many different patterns can be observed. For example, in arid areas, hypersaline conditions can exist in coastal systems. In very small estuarine systems with little freshwater input, such as the ''inlets'' of South Carolina, the salinity of the entire estuarine area may be essentially that of the adjacent sea. But, for most estuarine systems, there is a
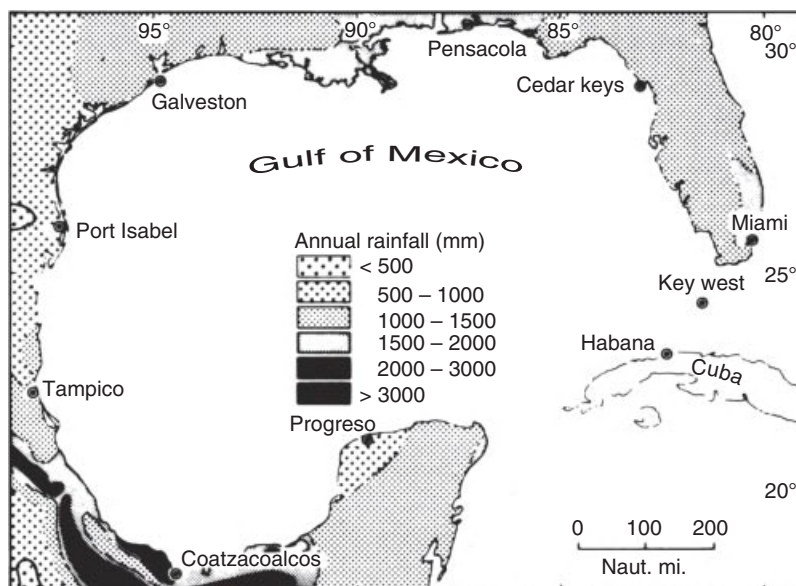
FIGURE 6.3 Average annual rainfall (mm) along the Gulf of Mexico coas. *Source*: From Smith and Monte (1975).

gradient in the mean salinity from near that of seawater at the coast to freshwater at some distance inland.

How does marsh vegetation change along this salinity gradient? In typical estuaries, there are broad vegetation zones, which are closely related to the salinity gradient. Nearest the coast, the community is dominated by salt marshes. The composition of this community changes with decreasing salinity until it is composed entirely of freshwater vegetation. This vegetation zonation has been described for many locations (Adams, 1963; Zedler, 1977; Bertness, 1992; Pennings and Callaway, 1992), and we include several examples here. In the Barataria Basin, Louisiana, there are several broad vegetation zones (Day et al, 1989). Nearest the coast there is a band of saline marsh, with zones of brackish marsh, freshwater marsh, and swamp forest progressively further inland. The plant diversity is lowest in the saline marshes and highest in the freshwater marsh; a pattern that holds for most estuaries. Similar patterns exist for the marshes of the Chesapeake Bay and other areas. However, a recent study in Chesapeake Bay (Sharpe and Baldwin, 2009) found that species richness in oligohaline marshes was as high as or higher than that in tidal freshwater marshes, resulting in a distinctly nonlinear pattern of plant species richness along the relatively undisturbed Nanticoke River. In contrast, the more urbanized Patuxent River gradient displayed a linear decrease in plant species richness with increasing distance downstream across the estuary. Hence, the authors conclude that the nonlinear pattern of plant species richness observed along the Nanticoke River

may be the typical pattern in relatively undisturbed estuaries.

6.3.3 Local Zonation Patterns

The striking patterns of marsh zonation that occur along tidal creeks have attracted the attention of wetland scientists for many years (Mendelssohn and Morris, 2000). These zones are a result of differences in reproduction and growth, response to environmental gradients encountered from low to high water, and plant competition. Some of the most important factors are elevation, drainage, and soil type. Tidal exchange and soil type are important in determining the oxidation–reduction state of the soil (Chapter 3) and the level of hypersaline conditions in the high marsh. In salt marshes, there is often a distinct elevation gradient from the water's edge up to the upland boundary and often a streamside levee. In the high marsh, salt pans (areas of hypersalinity) often form. An example of zonation across this gradient for marshes in New England is given in Figure 6.4.

A number of factors affect the distribution of vascular plant species along the estuarine gradient, including salinity, frequency and duration of inundation, sulfide concentration, and substrate composition (Odum, 1988; Mendelssohn and Morris, 2000; Fig. 6.5). On tidal coasts, low marshes are flooded daily by seawater, so the water and salinity regime of soils is rather independent of climatic conditions. For this reason, the low marsh areas of tidal Mediterranean-type climate coasts (i.e., California) have similar

(a)

(b)
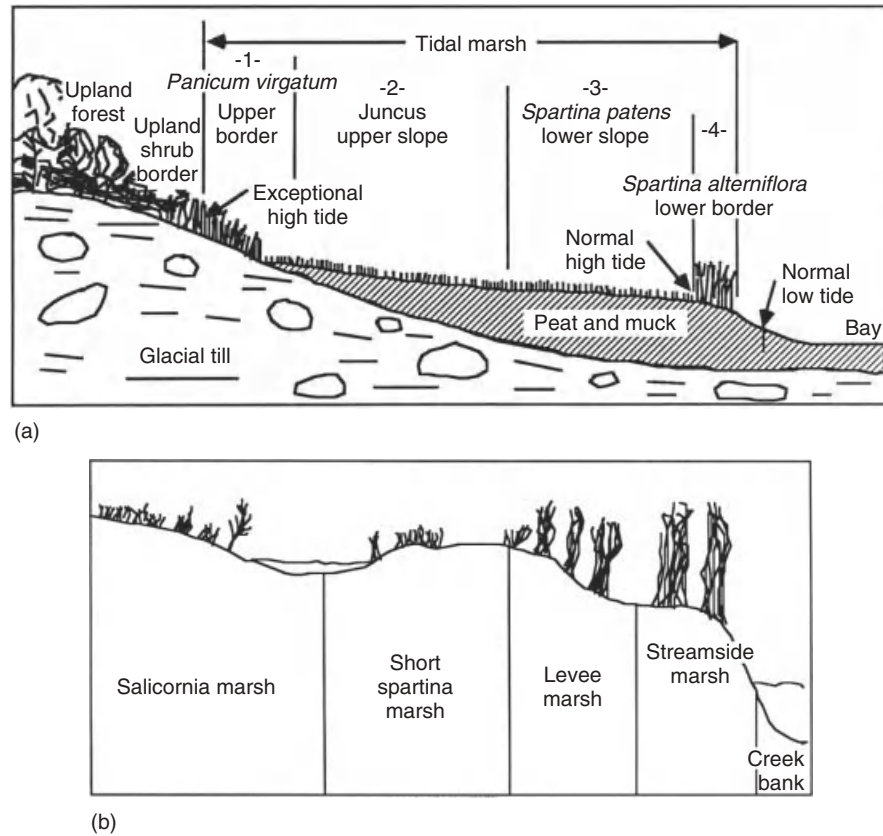
FIGURE 6.4 Zonation of vegetation in southern New England salt marshes. *Source*: From Bertness and Pennings (2000).

vegetation to that of the United States and the European temperate zone and it is composed of *Spartina* spp. communities. However, the middle and upper marsh areas are dominated by halophytes, often succulent chenopods, adapted to high soil salinity. Where hypersaline periods are too long, salt flats without perennial vegetation are widespread. In nontidal, Mediterranean-type coasts, low marshes dominated by *Spartina* spp. grasses are practically absent, and glasswort communities can develop from mean sea level to the upper marsh. Several authors have shown the importance of summer drought in explaining the distribution of plant communities in these areas (Zedler, 1983; Zedler and Beare, 1986; Callaway et al., 1990; Ibáñez et al., 2000).

There are differences in zonation of temperate tidal marshes, nontidal Mediterranean marshes, and tidal Mediterranean-climate marshes. On tidal coasts, factors responsible for marsh plant zonation are essentially similar to those causing zonation in the rocky intertidal zone. At the lower end of a physical gradient (low marsh), the range of a species is limited by its tolerance to physical conditions (i.e., submergence and hypoxia), whereas at the upper end of the gradient (higher in the marsh), a species is excluded by competition (Bertness and Pennings, 2000). Mediterranean-climate tidal salt marshes, however, do not exhibit a simple monotonic gradient of severity of physical factors across marsh elevations, rather there is an interaction between flooding and salinity that creates a band of superior habitat in the middle marsh, where both factors are moderate; a phenomenon not reported elsewhere (Pennings and Callaway, 1992).

Peinado et al. (1995) carried out one study comparing vegetation zonation of Mediterranean marshes in Spain and Mediterranean-climate macrotidal marshes in California and Baja California. The marshes in these two areas are similar in terms of taxonomic composition, physiognomy, and vegetation zonation. The low marsh is dominated by hydrophytic perennial vegetation: *Spartina* communities in the lowest subzone (which is practically absent in the Mediterranean basin due to low tidal range) and low *Sarcocornia* communities in the highest subzone. In the middle marsh, vegetation is mostly formed by erect species of *Sarcocornia*, and in the upper marsh by more halophytic species of the genus *Arthrocnemum*.
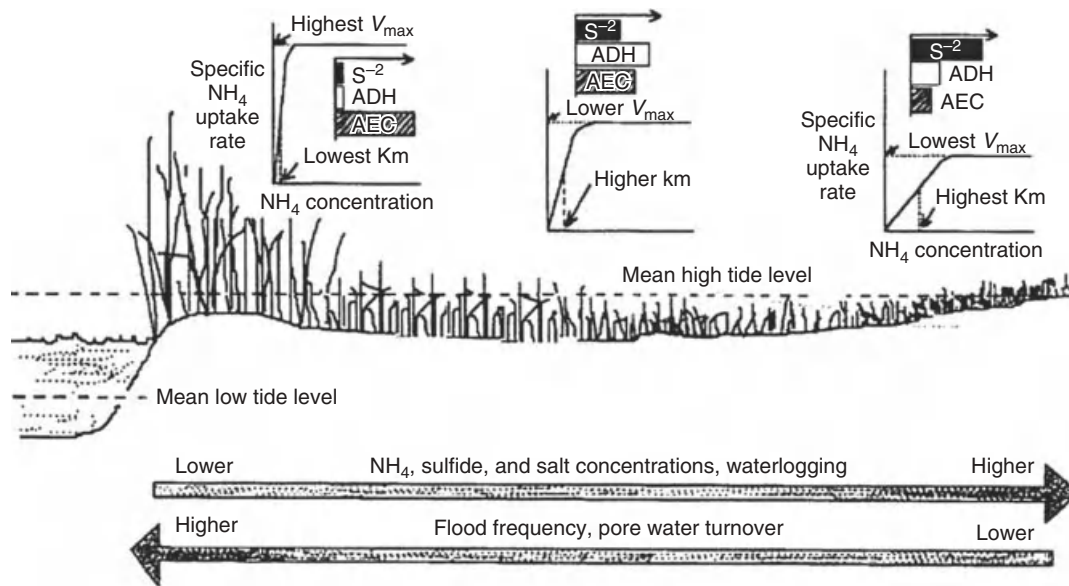
FIGURE 6.5 Factors affecting marsh biomass and production. Schematic of within-marsh variation in the height of *Spartina alterniflora* and the terms used to describe these height forms. See From Mendelssohn and Morris (2000) for further description of mechanisms.

Pioneer annual vegetation of *Salicornia* species can be found in the bare gaps. Finally, vegetation of the drier upper marsh is made up of halophytic tall rushes (*Juncus* spp.), which form the transitional zone between the marsh and upland vegetation.

In temperate tidal salt marshes, vascular plants are typically found only in the upper two-thirds of the intertidal zone. The lower one-third consists of bare mud and, at times, a layer of micro- and macroalgae. This lack of colonization is primarily a result of the high duration of flooding. Exceptions to this general pattern appear to occur where the tidal amplitude is very slight, as along the northern coast of the Gulf of Mexico. Here, marsh plants such as *Spartina alterniflora* often grow virtually to mean low tide (Odum, 1988). This is also true for the Mediterranean wetlands, where normally there are no tidal mud flats between the open water and the marsh.

6.4 STRUCTURE AND DYNAMICS: FACTORS AFFECTING BIOMASS AND PRODUCTIVITY

The factors affecting the productivity of salt marshes have been studied extensively; more so than those for mangroves. The majority of the existing studies are for

S. alterniflora, although there is considerable information available for other species (Hopkinson et al., 1978, 1980; Howes et al., 1981; Morris et al., 1990, 19901990; Clarke and Jacoby, 1994; Huckle et al., 2000; Ibáñez et al., 2000; Mitsch and Gosselink, 2001; Spalding and Hester, 2007). One reason that the productivity of salt marshes has been examined so thoroughly is that it is often remarkably higher than for most other ecosystem types. Another reason is that there is considerable evidence that marsh production forms the basis of important estuarine food chains (Deegan et al., 2000; Winemiller et al., 2007), although the controversy about nutrient subsidy from the marsh to the estuary (''outwelling hypothesis,'' Odum, 1968) still remains open (Weinstein and Kreeger, 2000).

There have been numerous studies of primary production in salt marshes but temporal and spatial variability limits generalizations (Odum, 1988). Most of the existing productivity values are for net production calculated from changes in live and dead plant biomass over an annual cycle. The data of such studies often look more or less like the examples given in Figure 6.6. Since most salt marshes are located in temperate climates, the live biomass increases during the growing season (spring until fall), then flowers and dies. As the grass dies, live biomass decreases and dead organic material increases. In the spring, the quantity of dead grass decreases as it decomposes. In lower latitude marshes, such as in Louisiana
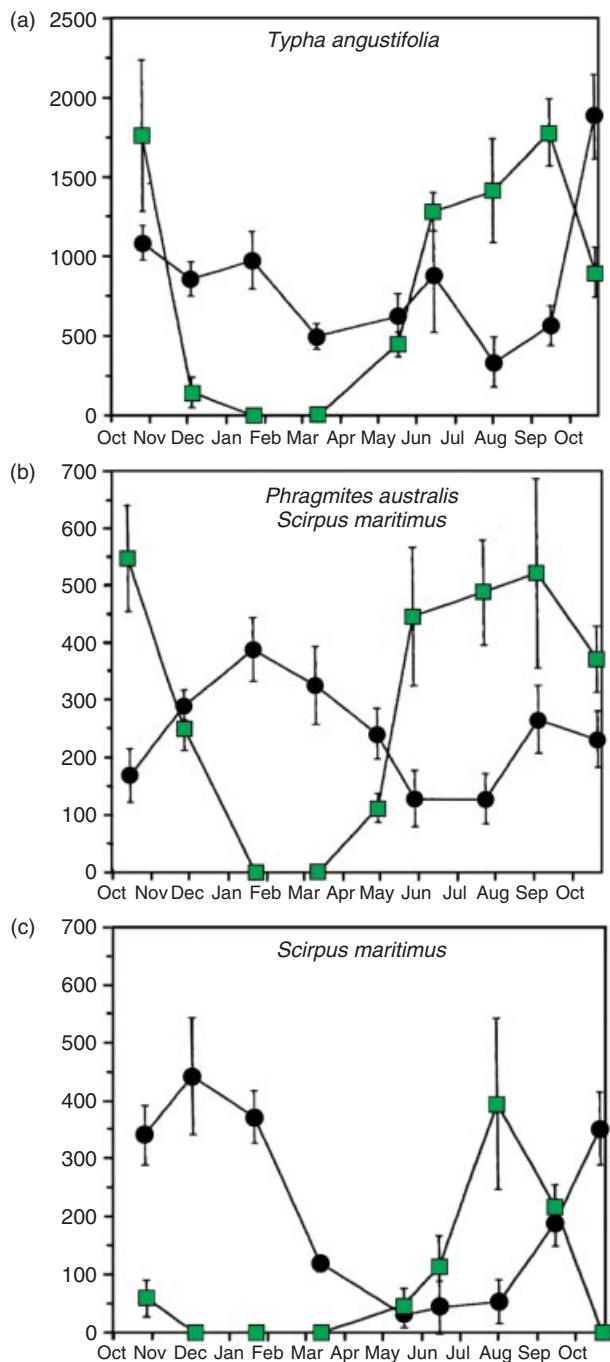
FIGURE 6.6 Seasonal patterns of aboveground live (green squares) and dead biomass (black dots) from three marshes in the Rhône Delta (France) dominated by different species. *Source*: From Ibáñez et al. (1999).

and Georgia, there is some growth year-round and live material is present at all times. In Louisiana, the live biomass of *S. patens* or *Juncus roemerianus* does

not change in any regular manner. In addition to these seasonal differences in marsh grass biomass, all marshes studied have distinct differences in both live and dead biomass between streamside and inland marsh locations, owing to factors such as variations in tidal flooding, nutrient chemistry, and oxygen content of the soil. All of them are treated in more detail.

Aboveground productivity estimates, mostly *Spartina* marshes from the Atlantic Coast of North America, range from 200 to 4000 $g/m^2/year$, and belowground estimates from 500 to 6200 $g/m^2/year$ (Turner, 1976; Kirby and Gosselink, 1976; Gallagher et al., 1980; Good et al., 1982; Morris and Haskin, 1990; Mendelssohn and Morris, 2000). Aboveground primary production of seven coastal marsh species in coastal Louisiana, a microtidal area with high temperature and rainfall, ranged from 1355 to 6043 $g/m^2/year$ (Hopkinson et al., 1978, 1980). Productivity values calculated from data on changes in marsh grass biomass range from less than 200 to greater than 6000 $g/m^2/year$ (Fig. 6.7). The aboveground net primary production (NPP) in freshwater tidal wetlands of the middle Atlantic coast ranges from 1000 to 4000 $g/m^2/year$, peak aboveground biomass from 566–2312 g/m^2, and belowground biomass from 500 to over 7100 g/m^2 (Whigham et al., 1978; Odum, 1988; Spalding and Hester, 2007).

There have been fewer studies of NPP of coastal Mediterranean marshes (Berger et al., 1978; Ibáñez et al., 1999, 2000; Curcó et al., 2002; Scarton et al., 2002). Table 6.3 compares the NPP values obtained in several studies carried out in the Mediterranean-type marshes. Aboveground values are higher in reed-type brackish marshes (with a maximum of 2989 $g/m^2/year$ in a *Typha angustifolia* marsh), while shrubby salt marshes show lower values (with a minimum of 94 $g/m^2/year$ in an *Arthocnemum macrostachyum* marsh). Aboveground NPP in reed-type marshes ranges from 452 $g/m^2/year$ in a *Scirpus maritimus* marsh to 2989 $g/m^2/year$ in the *T. angustifolia* marsh, both in the Rhone delta. In this case, the variation was mainly due to grazing in the *S. maritimus* marsh (the *T. angustifolia* marsh was protected by an enclosure).

Table 6.4 presents a detailed summary of marsh productivity of the Ebre (Ebro) delta, located in Catalonia (Spain). Soil features (organic matter, C and N content) and water and salinity regimes are more favorable for productivity in the brackish

TABLE 6.3 Net primary production estimates (grams per square meter) from different Mediterranean-type climate coastal marshes (brackish and salt marshes)

Marsh Type	Study Area	Location	Species	Above ground	Below ground	Method	Reference
Mediterranean							
Salt marsh	Po delta	Chioggia	*Sarcocornia fruticosa*	683	1260	Smalley	Scarton et al. (2002)
		Venice lagoon	*S. fruticosa*	347		Maximum standing crop	Caniglia et al. (1976)
	Rhône delta	Palissade	*S. fruticosa*	1123		Maximum standing crop	Ibáñez et al. (1999)
		Palissade	*S. fruticosa*	773		Maximum standing crop	Rioual et al. (1996)
		Digue South	*S. fruticosa*	1262		Maximum standing crop	Ibáñez et al. (1999)
		La Gacholle 4	*S. fruticosa*	1049		Maximum standing crop	Berger et al. (1978)
		La Gacholle 6	*S. fruticosa*	1000		Maximum standing crop	Berger et al. (1978)
		Digue North	*Arthocnemum macrostachyum*	187		Maximum standing crop	Ibáñez et al. (1999)
		Tour du Valat	*A. macrostachyum*	294		Maximum standing crop	Ibáñez et al. (1999)
		Bernacles	*A. macrostachyum*	94		Maximum standing crop	Rioual et al. (1996)
	Ebre delta	Buda 1	*A. macrostachyum*	190	50	Smalley	Curcó et al. (2002)
		Buda 2	*A. macrostachyum/S. fruticosa*	840	340	Smalley	Curcó et al. (2002)
		Buda 3	*S. fruticosa*	580	950	Smalley	Curcó et al. (2002)
Brackish marsh	Po delta	Barricata	*Phragmites australis*	876	2263	Smalley	Scarton et al. (2002)
	Rhône delta	Relongues in	*Typha angustifolia*	2989		Maximum standing crop	Ibáñez et al. (1999)
		Relongues out	*Scirpus maritimus*	452		Maximum standing crop	Ibáñez et al. (1999)
		Palissade	*P. australis/S. maritimus*	824		Maximum standing crop	Ibáñez et al. (1999)
	Ebre delta	Garxal	*P. australis*	1400	3740	Smalley	Curcó et al. (1996)
		Vilacoto	*Cladium mariscus*	1620	8070	Smalley	Curcó et al. (1996)

	Location	Species	Value	Method	Reference
California					
Salt marsh					
San Francisco bay	Mare Island	*Sarcocornia pacifica*	81–960	Maximum standing crop	Mahall and Park (1976)
	Petaluma River	*S. pacifica*	215–550	Maximum standing crop	Mahall and Park (1976)
Suisun marsh			276–722	?	Mall (1969)
San Francisco bay	Tolay Creek	*S. pacifica*	1060–1185	Maximum standing crop	Cameron (1972)
San Diego bay		*S. pacifica*	1500–2500	?	Mudie (1970)
South California	Several locations	*S. pacifica/Batis maritima*	300–1200	?	Cited in Rey et al. (1990)
San Diego bay		*Spartina foliosa*	800	?	Mudie (1970)
San Francisco bay	Petaluma River	*S. foliosa*	445–690	Maximum standing crop	Mahall and Park (1976)
	Mare Island	*S. foliosa*	280	Maximum standing crop	Mahall and Park (1976)
	Tolay Creek	*S. foliosa*	1400–1700	Maximum standing crop	Cameron (1972)
Tijuana Estuary		*S. pacifica*	632–729	Smalley	Zedler et al. (1980)
San Diego bay		*S. pacifica*	599	Smalley	Zedler et al. (1980)
Pe nasquitos lagoon		*S. pacifica*		Smalley	Zedler et al. (1980)
Florida					
Salt marsh					
Indian River Lagoon	Oslo Road Marsh	*S. pacifica/B. maritima*	1984–2316	Rey's method	Rey et al. (1990)
	North Marsh	*S. pacifica/B. maritima*	1139–1419	Rey's method	Rey et al. (1990)
	IRC&12 PD	*S. pacifica/B. maritima*	937–1413	Rey's method	Rey et al. (1990)
	IRC&12 UE	*S. pacifica/B. maritima*	835–1543	Rey's method	Rey et al. (1990)

Some estimates from subtropical marshes dominated by *Sarcocornia pacifica* and *Batis maritima* are also included (Ibáñez et al., 2000)

marshes, since in the salt marshes organic matter and nitrogen content are very low, and hypersalinity is present almost all year. Overall, there is an increase in the biomass and primary production as salinity decreases. The brackish marshes are dominated by reed-type species, which have a pronounced seasonality of the aboveground live biomass. Shrubby plants dominate the salt marshes and have a more constant aboveground live biomass during the year, an important part of which is lignified, nonphotosynthetic structures. Mean annual values of aboveground live biomass are quite homogeneous in three of the marshes (about 440–470 g/m^2), while the *Cladium* marsh (850 g/m^2) and the *S. fruticosa* marsh (1660 g/m^2) show higher values. In the salt marshes, maximum values of the aboveground NPP occur in the mixed marsh (840 g/m^2/year), which has an exceptionally high turnover, followed by the *S. fruticosa* marsh (580 g/m^2/year) and the *A. macrostachyum* marsh (350 g/m^2/year). Values of belowground mean live biomass, total biomass, litter, and production are very high in the two brackish marshes, especially in the *Cladium* marsh. Belowground NPP ranges from 3740 to 8070 g/m^2/year in the brackish marshes and from 50 to 950 g/m^2/year in the salt marshes.

The exchange of CO_2 between marsh plants and the atmosphere has also been used to measure production (Blum et al., 1978; Houghton and Woodwell, 1980; Hwang and Morris, 1994; Morris and Jensen, 1998; Neubauer et al., 2000). There are two types of exchange studies, one is by chamber, either open or closed, and the other is by eddy flux. This last technique allows the examination of daily and even hourly dynamics of marsh grass production. Figure 6.8 shows CO_2 exchange between a marsh and the atmosphere during the summer in New York when productivity was high. There is a net uptake of atmospheric CO_2 during the day when the plants are photosynthesizing and a net release at night when there is only respiration. The height of the tide also affects the rate of CO_2 exchange with the atmosphere. When the tide is high, more of the plant is covered and CO_2 exchange is with the water rather than with the atmosphere. Therefore, photosynthetic uptake from the air during the day and respiratory release at night are both lower during high tide. This does not necessarily mean that photosynthesis or respiration is lower, as some of the CO_2 exchange is with the water. But it does mean that the data must be interpreted with care.

Belowground production of marsh plants has been reported less often than aboveground production primarily because it is more difficult to measure

(Gallagher and Plumley, 1979; Good et al., 1982; Schubauer and Hopkinson, 1984; Groenendijk and Vink-Lievaart, 1987; Curcó et al., 2002; Scarton et al., 2002; Darby and Turner, 2008). In contrast with aboveground vegetation, it is often very difficult to distinguish live roots and rhizomes from dead and to determine distinct seasonal patterns. Productivity estimates for *S. alterniflora* range from 500 to 6200 g/m^2/year (Good et al., 1982; Darby and Turner, 2008). The ratio of the aboveground to belowground biomass for *S. alterniflora* ranges from 0.3 to 48.9 with most values being higher than 1, indicating that the belowground biomass is almost always considerably greater than aboveground biomass.

6.4.1 The Effect of Measurement Method on Productivity Results

As indicated above, there is a high degree of variability among marsh grass productivity values reported in the literature. This is partially a result of the different methods used. Our purpose here is not to evaluate these different techniques in detail but to suggest that the method must be known when considering different productivity values. It is also important to understand that different methods tell you different things. A good review of methods for estimating NPP of salt marsh macrophytes can be found in Morris (2007). A comparison of the different methods is also available in a number of articles (Turner, 1976; Kirby and Gosselink 1976; Hopkinson et al., 1978, 1980; Linthurst and Reimold, 1978; and Shew et al., 1981; Kaswadji et al., 1990; De Leeuw et al., 1996; Dai and Wiegert, 1996; Daoust and Childers, 1998).

The most commonly used production methods involve the harvest of live and dead grasses, done most simply by the harvest of peak end-of-season live standing material. Live material is continually dying, however, so that this end-of-season technique is an underestimate. More sophisticated methods include determining the changes in both live and dead standing crop at regular intervals and the use of techniques to estimate the loss of both dead and live material between sampling dates (Wiegert and Evans, 1964). Other techniques include different types of tagging to measure the increase in height, diameter, and number of leaves as well as the disappearance of individual plants and leaves (Hopkinson et al., 1978, 1980). As an example, Hopkinson et al. (1980) found that different techniques for measuring the annual net production of salt marsh plants in Louisiana gave highly variable results (Fig. 6.9). Kaswadji et al. (1990) measured the aboveground production of *S. alterniflora* in a Louisiana salt marsh using harvest methods as well as a nondestructive

TABLE 6.4 Productivity and other related parameters from several marshes of the Ebre delta (Ibáñez et al., 2000)

	Brackish Marsh	Brackish Marsh	Salt Marsh	Salt Marsh	Salt Marsh
Conductivity (mS/cm)	2.8	—	74.2	—	58.9
Water level (cm)	(2.3 0.7–6.0) (–41/22)	6.9 (1.1–13.9)	(37–145) –14.2	—	(23–87) –11.7
Number of soil layers	15	–2.1 (–20/26)	(–41/10)	—	(–31/10)
		15	—	—	10
Sampled thickness (cm)	60	30	—	—	20
Organic matter (%)	38.8	31.8	—	—	5.6
Carbon (mg/g)	235.2	168.3	—	—	50.1
Nitrogen (mg/g)	12.43	7.89	—	—	0.62
Species composition	*Cladium mariscus* (76%)	*Phragmites australis* (95%)	*Arthrocnemum macrostachyum* (99.2%)	*Sarcocornia fruticosa* (62%)	*Sarcocornia fruticosa* (100%)
	P. australis (12%)	*Scirpus maritimus* (5%)	*S. fruticosa* (0.8%)	*A. macrostachyum* (38%)	
Aboveground					
Mean live biomass (g/m^2)	850	470	470	440	1660
Total biomass (g/m^2)	2360	2060	730	950	2800
Litter (g/m^2)	1180	730	160	350	760
NPP (g/m^2/ year)	1620	1400	190	840	580
Turnover	1.9	3.0	0.4	1.9	0.3
Belowground					
Mean live biomass (g/m^2)	5100	2290	120	170	790
Total biomass (g/m^2)	7910	3700	140	250	940
Litter (g/m^2)	2870	1760	70	100	330
NPP (g/m^2/ year)	8070	3740	50	340	950
Turnover	1.6	1.6	0.4	2.0	1.2
Total					
Mean live biomass (g/m^2)	5950	2760	590	610	2450
Total biomass (g/m^2)	10270	5760	870	1200	3740
Litter (g/m^2)	4050	2490	230	450	1090
NPP (g/m^2/ year)	9690	5140	240	1180	1530
Turnover	1.6	1.9	0.4	1.9	0.6
Above–below ratio					
Mean live biomass	0.17	0.20	3.80	2.59	3.80
Total biomass	0.30	0.55	5.26	3.88	3.00
Litter	0.41	0.41	2.20	3.67	2.28
NPP	0.20	0.38	3.71	2.48	0.61

For water level and conductivity, the annual mean value and the range are shown. Species composition includes the % of biomass in relation to the mean (standing) biomass of the marsh.
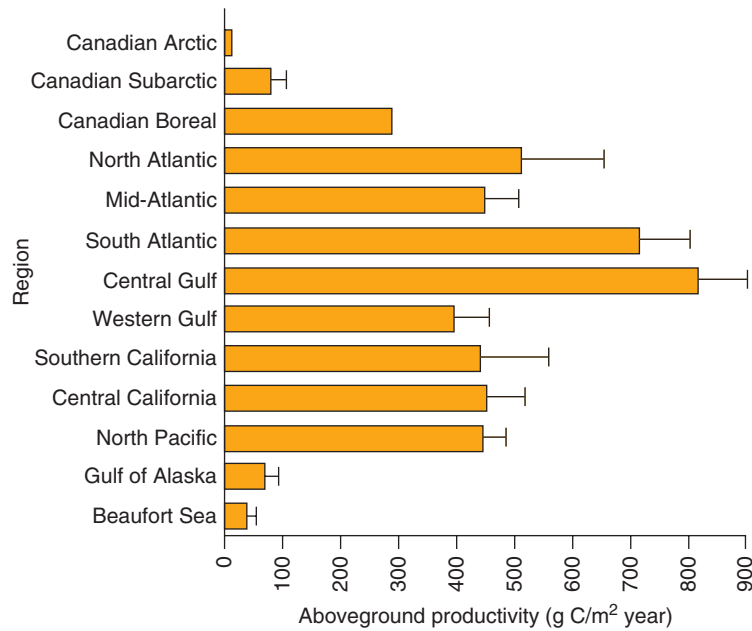
FIGURE 6.7   Salt marsh aboveground primary productivity by a region in North America, north of Mexico. *Source*: From Mendelssohn and Morris (2000).
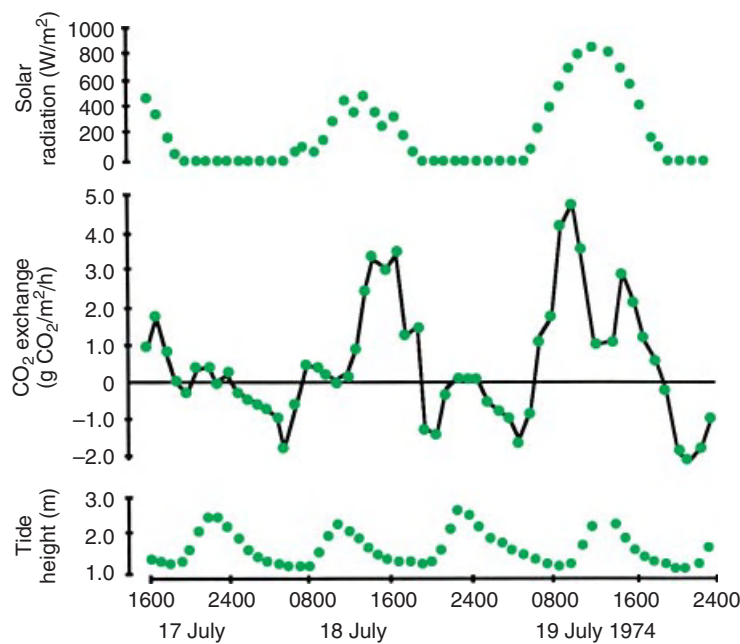
FIGURE 6.8   Solar radiation, atmospheric CO_2 exchange, and tide height for Flax Pond. *Source*: From the Flax Pond ecosystem study: exchanges of CO_2 between a salt marsh and the atmosphere, Houghton and Woodwell, Ecology, 1980, 61, 1434–1445. *Source*: Copyright by the Ecological Society of America, reprinted by permission.

method based on measurement of stem density and longevity. Annual production estimates ranged from 831 to 1873 g/m^2/year. It is generally considered that techniques that take into consideration changes in both live and dead standing material between sampling dates give the most accurate estimates of production. As a method of quantifying the NPP, allometric (nondestructive) methods that account for stem turnover are preferred over harvest methods (Morris, 2007).

As an alternative to harvest methods, fluxes of CO_2 and CH_4 have been used to estimate the gross and net macrophyte productivity under ambient field conditions (Blum et al., 1978; Howes et al., 1984; Whiting and Chanton, 1996) or under experimental conditions such as elevated atmospheric CO_2 concentrations (Rozema et al., 1991; Drake et al., 1997; Rasse et al., 2005; Marsh et al., 2005) or manipulated soil salinities (Hwang and Morris, 1994). The carbon gas flux technique integrates processes that occur within and between aboveground and belowground compartments (e.g., turnover and translocation) and therefore provides a more reliable estimate of the total production than that by harvest methods (Neubauer et al., 2000). If carbon fluxes from the sediments are measured *in situ*, the sediment microalgal production can also be calculated (Anderson et al., 1997). Morris and Jensen (1998) obtained a limit on the gross belowground production of 1310 $g/m^2/year$ from monthly measurements of canopy and soil CO_2 exchange in a Danish marsh. CO_2 exchange methods are useful for partitioning the gross primary production and for comparative purposes, but they are not well suited for routine monitoring of the NPP (Morris, 2007).

One promising technology is the application of light detection and ranging (LIDAR), which uses the same principle as radar (Morris, 2007). LIDAR has been used to map marsh terrain and canopy heights (Rosso et al., 2006), but further studies have to be developed to test the accuracy and feasibility of this technique.

6.4.2 Factors Affecting Marsh Production

A number of factors affect the productivity of coastal marshes. Flooding frequency and duration and soil salinity are perhaps the key factors, but temperature, rainfall, nutrient availability, oxygen levels, sediment type, and drainage are also important. These factors are interrelated and are in turn affected by plant growth (Mendelssohn and Morris, 2000; Fig. 6.5). Salt marshes can have significant interannual variation in productivity due to variation in the above factors (Teal and Howes, 1996). Some of these factors cause a difference in productivity over a latitudinal range, while others operate at the local level. In this section, we consider each of these factors separately, although obviously they act together.

6.4.2.1 Solar Radiation, Temperature, and Evapotranspiration

The energy of solar radiation affects photosynthesis in several direct and indirect ways. Solar energy directly energizes plant pigments so that the electromagnetic energy of light is converted into chemical potential energy. Solar radiation affects plants indirectly because changes in radiation lead to changes in temperature, and temperature directly affects the rate of metabolic processes. Heat energy is used to evaporate water and vascular plants obtain essential nutrients as a result because nutrients are moved from the soil to the leaves with this water. *Evapotranspiration*, as this process is called, is temperature dependent. Plants change their activity in response to changes in solar inputs, for example, as the day length increases or decreases.

Solar radiation, temperature, and evapotranspiration act together to produce differences in marsh production over a latitudinal gradient. This production gradient is not unexpected in view of our knowledge of other species. Geographic variations in the growth of plants with similar physiology, litterfall, and net ecosystem production are closely correlated to latitudinal factors, especially temperature and sunlight (Rosensweig, 1968; Bertness and Pennings, 2000; Asaeda et al., 2005). Low winter temperatures and the presence of ice affect the winter minimum biomass found in marshes. Along the Atlantic and Gulf coasts of North America, the minimum winter biomass decreases gradually from latitude 28 °N to 35 °N. Above 38 °N, the presence of ice generally prevents any winter biomass (Turner, 1976).

6.4.2.2 Tidal Range

The tide is one of the unique attributes of estuaries, and Odum (1974) called estuaries fluctuating water level ecosystems, which are subsidized by tidal action. Differences in marsh production, which apparently are related in some way to tidal effects, have been identified over broad areas with different tidal ranges as well as between streamside and inland marshes at many different sites. Steever et al. (1976) reported a strong correlation between tidal range and the peak standing crop of *S. alterniflora* along the Connecticut coast unrelated to the changes in climatic and edaphic factors. When they plotted data from various areas along the Atlantic coast with tidal ranges between 0.5 and 2.5 m, a relationship was evident (Fig. 6.10). In addition, they found that a ''gated'' marsh at Westport, Connecticut, had a lower peak standing crop than a nearby marsh where tidal exchange was not restricted. Steever et al. (1976) concluded that the data strongly suggest that the ''energy subsidy'' provided by tidal action is a significant factor in the standing crop production of *S. alterniflora*.
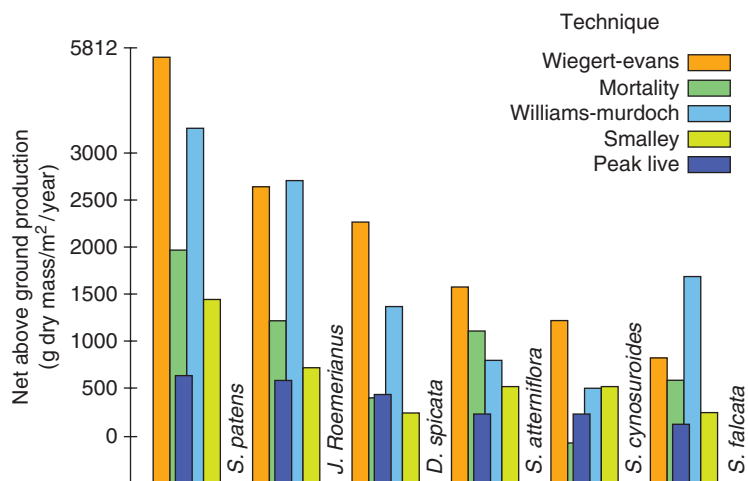
FIGURE 6.9 Estimates of annual aboveground production calculated from several widely used techniques. *Source*: From Hopkinson, Gosselink, and Parrondo, production of coastal Louisiana marsh plants calculated from phenometric techniques, Ecology, 1980, 61, 1091–1098. *Source*: Copyright by the Ecological Society of America, reprinted by permission.

A review on the relationship of *S. alterniflora* to tidal data can be found in McKee and Patrick (1988).

Spartina alterniflora production is not positively influenced by tidal action over an infinite range, because, at very high tidal ranges, the tide may become a stress. This is demonstrated in the Bay of Fundy where the tidal range exceeds 10 m and intertidal *S. alterniflora* is only 10–20 cm high. In addition, coastal Louisiana has a low tidal range (0.3 m) and very high productivity. This information and the scatter of points in Figure 6.10 indicate that still more factors are important in determining marsh productivity.

Tidal subsidies may also operate on a smaller scale. In almost all marshes, there is a striking difference between streamside and inland marshes. Turner (1979) showed that the difference between peak streamside and inland biomass was greater with greater tidal range. Much of the difference between streamside and inland marshes is related to the movement of water in the two areas. At low tide, water drains almost completely from the streamside marsh surface. In inland marshes, there is often incomplete drainage, leading to ponding and high salt levels during periods with high evaporation (Odum, 1980).

Another important factor in the drainage of marsh soils is the percolation rate (the rate at which water flows through the sediment surface into the deeper sediments). In a Massachusetts salt marsh, Howes et al. (1981) found that the relative percolation of water into sediments was inversely related to grass height. The barrier to water movement in the top 2 cm of the sediment was greatest where tall *Spartina*
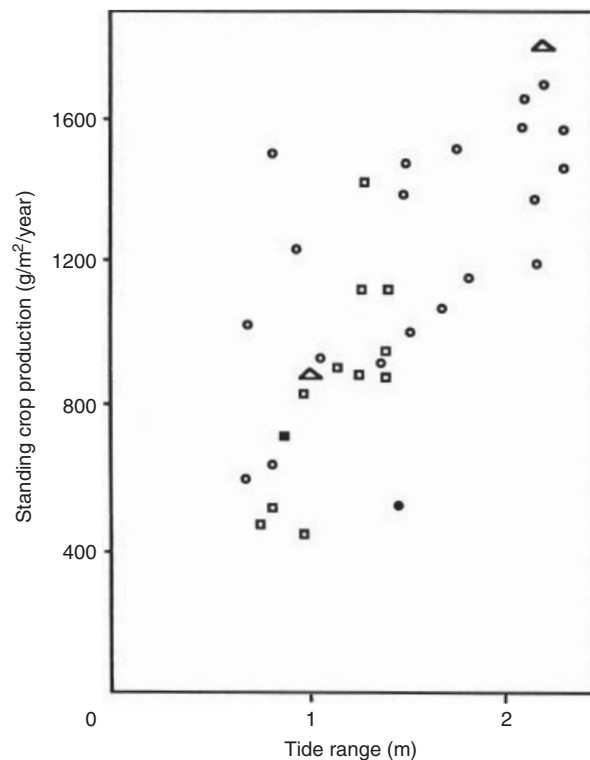
FIGURE 6.10 Production of intertidal *Spartina alterniflora* versus mean tide range for various Atlantic coastal marshes: Long Island Sound, Narragansett Bay, North Carolina, and Georgia. *Source*: From Steever et al. (1976).

grows. They hypothesized that fine sediments probably filled the sediment pores, forming a relatively impermeable layer on the surface. In addition, they found that the subsurface sediments of the streamside

region drained more rapidly at low tide than inland sediments. Thus, the combination of a relatively impermeable surface and well-drained sediments leads to high *Spartina* growth in the streamside zone. The situation in the inland marsh is just the opposite. Water flows freely through the surface, but the soils drain very poorly and growth of *Spartina* is less; a response shown experimentally by Mendelssohn and Seneca (1980). It is interesting that they also found tall *Spartina* in a narrow zone bordering the upland. Here, the water table is depressed because of the elevation of the site. They concluded that *Spartina* grows well where the root zone is not waterlogged. Many other factors that affect *Spartina* growth at the local level are also related to the differences in flooding and drainage. We examine these next.

6.4.2.3 Flooding Regime and Rainfall

Coastal marshes can be flooded either by marine water (meteorological and astronomical tides) or by freshwater (river floods, underground inputs, and rainfall). The timing and magnitude of seasonal oscillations in sea level seem to be the critical factors that influence salt marsh productivity (Morris et al., 1990). In a five-year study, Teal and Howes (1996) found that increasing sea level had a negative effect on the biomass of *S. alterniflora* in a salt marsh from Massachusetts. They found a relatively low degree of interannual change in biomass and primary production and concluded that year-to-year changes in production in more frequently flooded salt marsh areas may be less susceptible to variations in sea level. Conversely, in another five-year study, Morris et al. (1990) found that the annual aboveground productivity of *S. alterniflora* in a South Carolina salt marsh varied by a factor of 2 and correlated positively with anomalies in the mean sea level during the growing season. They concluded that the effect of sea level anomalies on the salinity of intertidal sediments probably accounted for the observed changes in the primary production. The higher salinity is a result of the combination of the lower flooding frequency and higher evapotranspiration (lower latitude) in relation to the Massachusetts salt marsh.

In a 13-year study carried out in a salt marsh in the Netherlands (De Leeuw et al., 1990), the authors found that year-to-year variation in peak aboveground biomass of six annual angiosperm communities could be explained by the rainfall deficit during the growing season, while inundation frequency did not contribute to the regression model. These authors suggested that the rainfall deficit may have influenced vegetation production through its impact on soil salinity and soil moisture content, and

they concluded that this effect increases with marsh elevation, where soil salinity is determined by the mutually opposing effects of evapotranspiration and precipitation. At tidal elevations below mean high water, fluctuations in soil salinity are strongly related to the salinity of the inundation waters and not to the rainfall deficit. Productivity of coastal Mediterranean marshes also seems to be strongly influenced by rainfall, owing to its effect in lowering soil salinity (especially in poorly flooded marshes), so they are more similar to the high marshes in the Dutch study. Mediterranean-type salt marshes are less productive, likely due to low rainfall during summer leading to salt and water stress. Other authors (Zedler, 1983; Dame and Kenny, 1986; Giroux and Bedard, 1987) have also attributed year-to-year differences in salt marsh production to climatic variability.

Temporary impounding can cause a decrease in production if rainfall is low and soil salinities increase, but it can also result in increased production if salinities drop because of high precipitation or upland runoff during the impounded period (Zedler et al., 1980). On the other hand, increased flooding may negatively affect production by decreasing sediment oxidation. Waterlogging is a key factor affecting redox potential, which in turn affects sulfide concentrations and the availability of nutrients in the soil to plants (Mendelssohn and McKee, 1988; Pennings and Callaway, 1992; Mendelssohn and Morris, 2000).

6.4.2.4 Salinity

Salinity is also an important determinant of salt marsh growth (Adams, 1963). Adams also reported that soil salinities of 70 ppt prevented the establishment and survival of most salt marsh species. On the other hand, *S. alterniflora* grown in freshwater becomes chlorotic, and the best growth is at 10 ppt salinity. Linthurst (1980) reported that, although the growth of *S. alterniflora* was less at 30 and 40 ppt, growth at these salinities was stimulated by aeration and nitrogen additions. At high salinities, osmotic stress (resulting in reduced water uptake) and cell membrane damage are likely to limit growth. Membrane permeability changes can reduce the influx of necessary nutrients and/or cause leakage of nutrients from the roots to the surrounding substrate. Increased permeability may also decrease the effectiveness of any selective ion uptake mechanisms in addition to increasing the potential for losses of needed oxygen from the roots (Linthurst, 1980). Halophytes seem to deal with osmotic stress by selectively concentrating preferred ions while making metabolic adaptations to the high concentrations of ions. In addition, these plants have the capacity for salt removal via salt

TABLE 6.5 Salinity values for optimum growth for several halophytes

Species	Optimum Growth (ppt NaCl)	Reference
Sarcocornia fruticosa	10	Grouzis (1973)
S. fruticosa	12.3–24.6	Abdulrahman and Williams (1981)
Sarcocornia perennis	0	Adams and Bate (1994)
Sarcocornia natalensis	21.6	Naidoo and Rughunanan (1990)
Salicornia emerici	10	Grouzis (1973)
Salicornia patula	3	Grouzis et al. (1977)
Salicornia brachystachya	3	Grouzis et al. (1977)
Salicornia rubra	12.3–24.6	Tiku (1976)
Salicornia bigelovii	14.4	Webb (1966)
S. bigelovii	3.6–7.2	Ayala and O'Leary (1995)
Salicornia dolischostahya	3.6–7.2	Rozema (1991)
Suaeda maritima	3.6–7.2	Rozema (1991)
Halimione portulacoides	3.6–7.2	Rozema (1991)
Atriplex nummularia	3.6–7.2	Rozema (1991)

glands and a mechanism in the roots for slowing the inward penetration of toxic ions. The result of this process is readily observed in the form of the salt deposits found on the leaves of *S. alterniflora* and in other halophyte species (Ibáñez et al., 2000).

Usually, the optimal salinity for maximum salt marsh growth is in the range of 100–200 mM (7.2–14.4 ppt), and the growth is significantly reduced as salinity increases or decreases (Table 6.5). *Salicornia bigelovii* is a succulent annual species that occurs in coastal estuaries and is reported to have maximum growth at about 14 ppt. The deleterious effects of salinity are assumed to result from water stress, ion toxicities, ion imbalance, or a combination of these factors (Ayala and O'Leary, 1995). These authors also concluded that the reduced growth at suboptimal salinity is apparently neither due to an insufficient supply of photosynthate to support growth nor is it due to less than favorable water relations in the shoots as had been suggested earlier, but it rather seems as

if the growth differences may be more closely related to differences in ionic relations.

In one greenhouse experiment, Rozema (1991) found that with 17 halophytic species only those from the genera *Salicornia* and *Suaeda* showed an increase in the mean relative growth rate under saline conditions. Chenopodiaceae species such as *Atriplex nummularia*, *Suaeda maritima*, *Halimione portulacoides*, and *Salicornia dolichostachya* have been found to have maximum growth rates where the external salinity is 50–100 mM NaCl (3.6–7.2 ppt) (Rozema, 1991). Rozema discussed the suboptimum growth of different Chenopodiaceae species from saline habitats and suggested that unfavorable water relations (the overall water balance of the plant) at 0 mM NaCl are implicated in the growth reduction. Salinity is necessary to maintain the turgor pressure potential required for growth.

Zedler (1983) found that a short-term reduction in the salinity of normally hypersaline soils was followed by a 40% increase in the August biomass of *Spartina foliosa* at the Tijuana estuary (southern California) and that a longer period of brackish water influence in Los Peasquitos lagoon was followed by a 160% increase in the August biomass of *Sarcocornia pacifica*. The largest increase in salt marsh biomass occurred in a nontidal lagoon with a relatively small increase in stream discharge, while tidal marshes underwent lesser changes in biomass following major flooding events.

6.4.2.5 Other Factors Affecting Marsh Productivity at the Local Level

A number of factors affect the growth of salt marsh plants within a local area. These include nutrient levels (such as the concentration of N, P, and Fe), the pH and *Eh* of the soil, waterlogging and drainage of the soil, oxygen levels, sediment type, herbivory, and competition, among others. These factors are interrelated and affect plant growth and in turn are affected by it. Ibáñez et al. (2000) and also Mendelssohn and Batzer (2006) provide reviews of these factors. Since nutrients are one of the most important factors limiting plant growth, we begin our discussion with this subject.

Although there is no consensus on the details, a general model has emerged that *S. alterniflora* is generally limited by N availability and that N availability on a physiological level is dictated by the presence of salts, sulfides, and oxygen that modify the kinetics of N uptake (Morris, 2007). Studies over a wide geographic range have shown that the

addition of inorganic nitrogen (but seldom inorganic phosphorus) increases the growth of *S. alterniflora* and other species (Sullivan and Daiber 1974; Valiela and Teal, 1974; Patrick and DeLaune, 1976; Mendelssohn, 1979a, 1979b; Buresh et al., 1980; Morris, 1991; Kiehl et al., 1997; Leendertse et al., 1997; Rozema et al., 2000; Deegan et al., 2007; Bertness et al., 2008).

These results clearly show that the plant macronutrient that most limits *Spartina* growth is nitrogen. However, other studies show that additional factors affect nitrogen uptake by plants. For example, in both Louisiana and Georgia marshes, nitrogen addition gave a greater response in inland marshes than it did in streamside marshes (Buresh et al., 1980). These and other studies in Louisiana, North Carolina, and Massachusetts have shown that ammonia levels were higher in inland marsh soils, although *Spartina* growth was less (Mendelssohn, 1979a, 1979b; Valiela and Teal, 1974, 1979; Buresh et al., 1980; Craft et al., 1991; Mendelssohn and Morris, 2000). Thus, higher nitrogen does not necessarily mean greater plant growth (Turner et al. 2009). Some other factors can help explain these results.

The amount of oxygen present in marsh soils is an important factor affecting plant growth. Maximum growth of *S. alterniflora* occurs in oxygenated soils, and the H_2S produced in anaerobic sediments inhibits respiration and nutrient uptake (Mendelssohn and Morris, 2000). Marsh soils, however, are almost completely anaerobic. How then do *Spartina* and other marsh plants achieve such high growth? The answer to this question is a function of both plant metabolism and the drainage characteristics of marshes. The pH of the soil also affects plant growth. Linthurst (1980) reported that the growth of *Spartina* was optimal at pH 6 in comparison to a pH of either 4 or 8. The ecophysiological response of marsh plants to stress factors is explained in the following section.

The nature of the soil in marshes affects the growth of marsh plants. Fine-grained c1ay and silty c1ay soils have higher nutrient levels than sandy soils and support greater growth of marsh grasses. Soil density is highest in streamside marsh soils because of the input of mineral sediments during high tide. DeLaune et al. (1979) found in Louisiana that the aboveground standing crop of *S. alterniflora* was correlated with soil bulk density. This correlation was apparently a result of the association of this property with the content of mineral matter in the soil. They also found that the input of nutrients with new sediments was the most important source of ''new''

nutrients for the salt marsh. Since the sedimentation rate is much higher on streamside marshes, this is a contributing factor causing higher productivity (due to better soil drainage) compared with marshes further inland. Craft (2007) found that tidal fresh and brackish marsh soils across all geographic regions of the contiguous United States had significantly lower bulk density and greater percent organic C, N, and P than salt marshes and that vertical accretion and N accumulation were negatively correlated with salinity.

Some studies indicate that the age of a plant stand affects its productivity (Bertness, 1987). These finding suggest that, as a marsh ages, there is increasing belowground biomass, especially of refractory organic materials. Nutrients become tied up as organic nutrients in the biomass and are less available for new plant growth.

Herbivory can also affect the growth of marsh grasses. Early studies in North American salt marshes concluded that plant–herbivore interactions were of little consequence to community dynamics and productivity (Teal, 1962; Marples, 1966). The prevailing paradigm in marsh ecology for nearly five decades has been that bottom-up forces are the primary determinants of plant production (Mitsch and Gosselink, 2001). Recent research on the East Coast of the United States from Virginia to Louisiana (Silliman and Zieman, 2001; Silliman and Bertness, 2002; Silliman et al., 2005), which employed grazer exclusion experiments, has challenged the current marsh theory and suggests that powerful trophic interactions can influence the high primary production observed in these communities. These authors showed that (i) the snail *Littoraria* strongly suppresses cordgrass production everywhere on the marsh surface (both short-form and tall-form *Spartina* zones) where it reaches high densities and (ii) snail-grazing impacts are strongest in the N-rich, tall-form *Spartina* zone. They also suggested that predators (mostly blue crab), by controlling snail densities, indirectly facilitate the high levels of primary production observed in salt marsh communities. These findings have important implications for the long-term conservation of salt marshes, since intense fishing off the East Coast of the United States has led to depleted densities of predators in estuarine communities (Silliman and Bertness, 2002).

Competition is also a factor affecting marsh productivity. In southern California, Pennings and Callaway (1992) showed that the growth of *S. pacifica* and *Arthrocnemum subterminalis* was negatively affected by flooding, salinity, and competition. However, the

TABLE 6.6 Services provided by coastal wetlands

Services	Comments and examples	Estuaries and marshes	Mangroves	Lagoons, including salt ponds	Intertidal flats, beaches, and dunes	Kelp	Rock and shell reefs	Seagrass beds	Coral reefs
Coastal Wetlands									
Provisioning									
Food	Production of fish, algae, and invertebrates	●	●	·	●	·	●	·	●
Freshwater	Storage and retention of water; provision of water for irrigation and for drinking	·		·					
Fiber, timber, fuel	Production of timber, fuelwood, peat, fodder, and aggregates	●	●	●					
Biochemical products	Extraction of materials from biota	·	·				·		·
Genetic materials	Medicine; genes for resistance to plant pathogens, ornamental species, and so on.	·	·	·		●			·
Regulating									
Climate regulation	Regulation of greenhouse gases, temperature, precipitation, and other climatic processes; chemical composition of the atmosphere	●	●	●	·		·	·	●
Biological regulation (C11.3)	Resistance of species invasions; regulating interactions between different trophic levels; preserving functional diversity and interactions	●	●	●	·		·		·
Hydrological regimes	Groundwater recharge/discharge; storage of water for agriculture or industry	·		·					
Pollution control and detoxification	Retention, recovery, and removal of excess nutrients and pollutants	●	●	●		?	·	·	·
Erosion protection	Retention of soils	·	●	·				·	·
Natural hazards	Flood control; storm protection	●	●	·	·	·	●	●	●
Cultural									
Spiritual and inspirational	Personal feelings and well-being	●	·	●	●	·	·	·	●
Recreational	Opportunities for tourism and recreational activities	●	·	·	●	·			●
Aesthetic	Appreciation of natural features	●	·	●	●				●
Educational	Opportunities for formal and informal education and training	·	·	·	·		·		·
Supporting									
Biodiversity	Habitats for resident or transient species	●	●	·	●	·	●	·	●
Soil formation	Sediment retention and accumulation of organic matter	●	●	·	·				
Nutrient cycling	Storage, recycling, processing, and acquisition of nutrients	●	●	●	·	·	·		●

Source: Millennium Ecosystem Assessment (Finlayson et al.,2005).

relative importance of these factors to the plants varied across the marsh. Thus, the benefit of reduced flooding in the *Arthrocnemum* zone outweighs the disadvantage of higher salinity and consequent lower water potential, and both species grow better in the *Arthrocnemum* zone than in the low *Sarcocornia* zone. In contrast, both species do poorer in the transition zone than in the *Arthrocnemum* zone, even though flooding is greatly reduced, probably because of the high salinity of the transition zone soil. Similarly, although removal of competitors usually increased plant growth dramatically, *Arthrocnemum* plants in the low *Sarcocornia* zone did not have high productivity, presumably because of harsh physical conditions.

A final major factor that is partly responsible for the high productivity of salt marshes is that many species of salt marsh plants have the C4 biochemical pathway of photosynthesis. C4 plants have, as a group, higher levels of production than most other plants (C3 plants). The designation refers to the number of carbon atoms in the initial product of photosynthesis, which is phosphoglycerate acid for C3 plants and malate acid for C4 plants. The details of the biochemistry of the two pathways can be found elsewhere (Mitsch and Gosselink, 2001). The response of these two types of plants to different environmental parameters is of interest here. C4 plants have much higher light and temperature saturation levels than C3 plants. For example, the summer temperature optimum for *S. alterniflora* (a C4 plant) is 30–35 °C, while that for *J. roemerianus* (a C3 plant) is 25 °C (Giurgevich and Dunn, 1979). This means that, as the temperature or light rises, the photosynthesis rate for C3 plants levels off earlier than for C4 plants. There is also less water transpired per unit photosynthesis in C4 plants. This could be important in limiting salt buildup on the leaf surface when transpiring salty estuarine water. Most C3 plants exhibit levels of photorespiration that are higher relative to photosynthesis than C4 plants. For example, photorespiration for *S. alterniflora* is 11–40% of photosynthesis, while that for *J. roemerianus* is 54% (Giurgevich and Dunn, 1979). Since many salt marsh species (including *Spartina* sp. and *Distichlis* sp.) are C4 plants, this leads to generally high marsh productivity.

6.5 ECOPHYSIOLOGICAL RESPONSE OF MARSH VEGETATION TO STRESS FACTORS

Considerable attention in salt marsh ecology, especially during the 1970s, was directed at understanding the nutrients that limit the growth of *Spartina* (Sullivan and Daiber, 1974; Broome et al., 1975; Gallagher, 1975; Valiela and Teal, 1974; Mendelssohn, 1979a). Fertilization experiments have consistently demonstrated that, in areas of low productivity, short *Spartina* can be stimulated by the addition of inorganic nitrogen, that is, ammonium or nitrate (Mendelssohn, 1979a). Phosphorus can be the primary nutrient limiting the productivity of *Spartina* growing on sandy substrates (Broome et al., 1975) and can also be secondarily limiting in some marshes. For example, in a South Carolina salt marsh, there was no growth response from *Spartina* in plots treated only with phosphorus, but the combination of phosphorus- and nitrogen-stimulated growth to a greater extent than nitrogen alone, which indicates that phosphorus becomes limiting when nitrogen loading exceeds a threshold (Morris, 1988). Although some earlier investigations have suggested that iron may limit *Spartina* growth (Adams, 1963), experimental documentation is lacking (Broome et al., 1975). However, there are strong biogeochemical interactions among iron, phosphorus, and sulfide that may well determine the availability of both iron and phosphorus to salt marsh vegetation.

By the 1970s, the scientific evidence was strong that nitrogen deficiencies limit the growth of *Spartina* in the same way that nitrogen scarcities limit the growth of phytoplankton in marine and estuarine environments (Valiela, 1995). However, other evidence based on whole marsh nitrogen budgets and standing stocks suggested that nitrogen limitation was a more complex phenomenon than first imagined. Investigations quantifying plant-available inorganic nitrogen concentrations along the *Spartina* productivity gradient documented that interstitial ammonium, the dominant inorganic nitrogen form in most salt marshes, was often an order of magnitude higher in the less productive inland (short) *Spartina* zone than in the more productive streamside (tall) zone (Craft et al., 1991; Mendelssohn, 1979b). Later, it was shown that pore water concentrations of ammonium in marshes are more than an order of magnitude more concentrated than the combination of ammonium and nitrate in tidal water (Mendelssohn and Morris, 2000). Thus, the diffusion gradient for ammonium, the dominant form of nitrogen in marsh sediments, is from the sediment to the surface water, suggesting that the sediment produces a surplus of ammonium nitrogen. Likewise, research on the nitrogen budgets of marsh ecosystems was beginning to show that salt marshes exported more inorganic nitrogen through tidal exchange than was imported (Valiela and Teal, 1979). Thus, nitrogen seems to be present in abundance in

salt marsh environments, but *Spartina* is apparently incapable of taking advantage of it.

Beginning in the 1980s, research was beginning to point to a link between the physiology of nitrogen uptake in *S. alterniflora* and the biogeochemical properties of the soils. Researchers established a positive relationship between ammonium uptake and oxygen in hydroponic cultures (Morris, 1984; Morris and Dacey, 1984). The rate of uptake under anaerobic conditions was approximately 50% lower than that found in O_2-saturated treatments (Morris, 1984). Although *S. alterniflora* has a well-developed aerenchyma (airspace) system, it is not able to alleviate root oxygen deficiencies in the more biochemically reduced zones of the marsh (Mendelssohn et al., 1981). There was also growing evidence that H_2S toxicity may contribute to the development of growth forms of *S. alterniflora* by inhibiting ammonium uptake (King et al., 1982; DeLaune et al., 1983; Morris, 1984; Mendelssohn and McKee, 1988; Koch and Mendelssohn, 1989; Bradley and Morris, 1990), and it was confirmed that H_2S at concentrations typical of those found in salt marsh sediments had the effect of lowering the V_{max} and raising the K_m for ammonium uptake. Furthermore, H_2S inhibits the anaerobic production of energy, thus providing a mechanism for the effect of H_2S on nitrogen uptake kinetics (Koch et al., 1990). Salt water cations such as sodium can also affect the uptake of ammonium by competing for carriers of ammonium on the root membrane. At salinities typical of salt marshes, this has the effect of lowering the K_m for ammonium uptake and reducing the efficiency of the uptake mechanism by the roots (Bradley and Morris, 1991). Also, in response to high salinity, *S. alterniflora* produces nitrogenous organic solutes (e.g., proline and glycinebetaine), which help in osmotic adjustment, but reduce the nitrogen available for plant growth (Cavalieri and Huang, 1981).

Nutrient absorption across root membranes is an active metabolic function that requires the consumption of oxygen (Epstein, 1972). The anatomy of *Spartina* allows for diffusion of oxygen to the root system (Arenovski and Howes, 1992; Howes and Teal, 1994; Teal and Kanwisher, 1966). This is an adaptation that is typical in wetland plants (Armstrong, 1979). In *Spartina*, the movement of oxygen into the root system is aided by the process of hygrometric pressurization (Hwang and Morris, 1991), but in the absence of a supply of oxygen in the soil, the rate of internal oxygen transport within the plant is apparently insufficient to promote a highly efficient nutrient uptake mechanism (Morris and Dacey, 1984), and root anaerobic metabolism may occur (Mendelssohn and McKee,

1987; Mendelssohn et al., 1981). For reasons that are not understood, the convective flow of gas through *Spartina* does not approach that of *Phragmites* or *Typha* (e.g. Brix et al., 1992). Under anoxic conditions, the production of energy via aerobic root respiration is impaired, and root alcoholic fermentation, the dominant pathway of anaerobic carbon metabolism in plants (Ap Rees, 1974), becomes the primary energy source in flood-adapted plants. Thus, the ability of *Spartina* to maintain high rates of alcoholic fermentation during root hypoxia/anoxia is of paramount importance to its growth and survival in flooded environments (Mendelssohn et al., 1981; Mendelssohn and McKee, 1987; Mendelssohn and Morris, 2000).

6.6 FACTORS AFFECTING MARSH ACCRETION AND HABITAT CHANGE

Coastal marshes are known to have maintained an elevation in equilibrium with mean sea level for thousands of years (Redfield, 1972). They do this by accumulating mineral sediment and organic matter (Stevenson et al., 1986). Interestingly, some marshes, common in New England, are peat dominated and apparently maintain elevation primarily by accumulating organic matter, while other marshes primarily accrete mineral sediment. The details of how they accomplish this in some cases, and not in others, and how and where they equilibrate within the tidal frame are currently areas of active research. Commonly, stable intertidal salt marshes occupy a broad, flat expanse of landscape often referred to as the *marsh platform* at an elevation within the upper part of the intertidal zone (Krone, 1985). Marsh vegetation, however, is known to grow at a wide range of elevations spanning the tidal range (McKee and Patrick, 1988; Day et al., 1999).

Recent work has shown that the relative elevation of the salt marsh surface is an important variable that controls the productivity of the salt marsh plant community. Moreover, the productivity or biomass density, in turn, influences the rate of accretion of the marsh surface (Morris et al., 2002; Kirwan and Murray, 2007; Mudd et al., 2009; Kirwan et al., 2010; D'Alpaos, 2011). The elevation of the marsh platform relative to mean high water and mean sea level determines the inundation frequency, duration and, consequently, wetland productivity (Fig. 6.11). There is a species-specific optimum elevation and hydroperiod for marsh vegetation, and, at superoptimal

elevations, an increase in the mean sea level relative to the marsh surface will stimulate growth (Morris and Haskin, 1990). The sedimentation rate is affected positively by the biomass density of marsh vegetation due to the drag exerted by the plant canopy (Leonard and Luther, 1995; Christiansen et al., 2000; Morris et al., 2002). Hence, in response to rising sea level, an increase in biomass density will increase sedimentation rate, thereby raising the elevation of the marsh. Also, with increased plant growth, belowground productivity, which also contributes to elevation change (McKee et al., 2007), may increase. The equilibrium elevation is inversely related to the rate of sea level rise and subsidence. That is, when rates of sea level rise and/or subsidence increases, the equilibrium elevation will decrease. One implication of this feedback is that a vegetated marsh is only stable when its elevation is superoptimal, because at suboptimal elevations an increase in sea level will depress growth and, thus, sedimentation. Marsh species or communities typically segregate along gently sloping topographic gradients on the marsh platform. The competitive balance among species is determined largely by the relative elevation of a site (Bertness, 1991; Pennings et al., 2005), and the outcome determines primary production as well as the sedimentation rate. There are intraspecific differences among marsh macrophytes in their effect on the sedimentation rate. For example, Leonard and Luther (1995) demonstrated that *J. roemerianus* and *S. alterniflora* at equal densities have significantly different effects on the turbulence intensity of the floodwater over a marsh, which has a great effect on sedimentation and erosion. Thus, the net sedimentation rate is a function of species composition and, as noted above, productivity and biomass density. Therefore, the competitive interactions among plant species are mediated by the influence of the vegetation on sediment accretion and modifications to the relative elevation of the marsh surface (Morris, 2006). More detail on the response to sea-level rise can be found in chapter 20 on climate change.

6.7 FUNCTIONS, VALUES, AND ASSESSMENT OF COASTAL MARSHES

From an ecological standpoint, wetlands perform a wide variety of functions at a hierarchy of scales ranging from the specific (e.g., nitrogen retention) to the more encompassing (e.g., biogeochemical cycling)
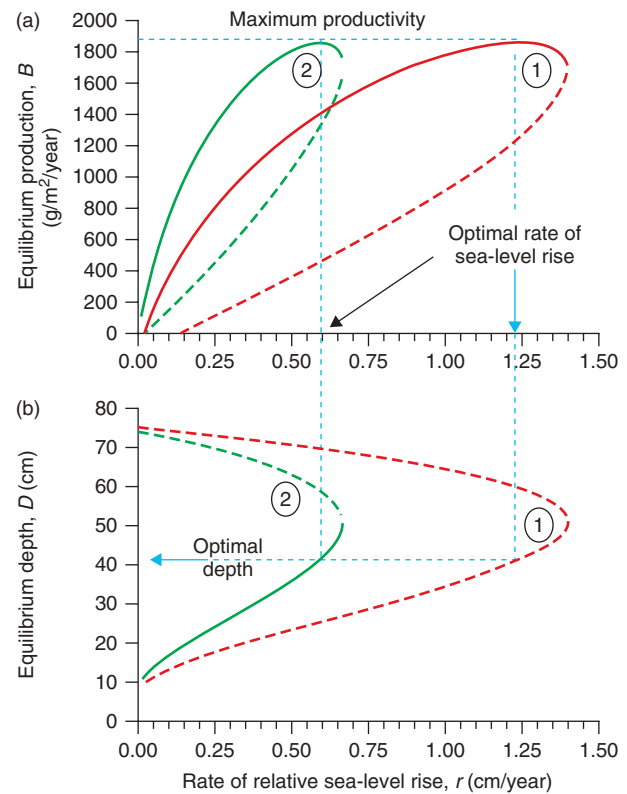
FIGURE 6.11 Equilibrium combinations of (a) productivity and (b) depth below mean high tide (MHT) as functions of the rate of relative sea level rise, for estuaries characterized by (i) high and (ii) low sediment loading. The optimal depth is the depth below MHT that results in maximum productivity. *Source*: From Morris et al. (2002).

as a result of their physical, chemical, and biological attributes. At the highest level of this hierarchy is the maintenance of ecological integrity, the function that encompasses all ecosystem structure and processes. The link between function and condition lies in the assumption that ecological integrity is an integrating ''super'' function of wetlands. If the condition is excellent (i.e., equal to reference condition or some ''ideal'' condition), then the ecological integrity of the wetland is intact and the functions that are typical of that wetland type also occur at reference levels (Fennessy et al., 2004). A detailed list of functions, values, and services provided by coastal wetlands is shown in Table 6.6.

The assessment of the wetland condition, based on a set of indicators, is necessary to quantify the ecological status of the ecosystem and its deviation from reference conditions. According to the results of the assessment, scientists and managers can have guidance to establish restoration and management measures to improve the wetland condition. Nowadays,

there is a large number of assessment methods world-wide, especially in the United States and the European Union. Table 6.7 shows a list of rapid assessment types and possible outputs for different purposes.

6.7.1 Indicators of Coastal Marsh Stability and Productivity

The health and productivity of coastal wetlands are dependent on the success of the plant life, which in turn is dependent on the plants' relationship to sediment, sea level, and the tide. Many coastal marshes depend on sediments supplied by rivers to counter-act the effects of land subsidence, sea level rise, and sediment compaction. In some areas, changes on the land have led to reduced riverine sediment supply to marshes, leading to a decrease in height relative to the mean sea level. Where dams or levees have been constructed to prevent flooding, marshes have been cut off from their source of sediment, and the net effect is conversion of marsh habitat to open water (Day et al., 2007).

Vertical elevation is a critical variable that determines the productivity and stability of salt marshes. The long-term existence of the salt marsh depends on the success of the dominant plants, such as *Spartina* and *Juncus* spp., and their close relationship to sediment supply, sea level change, and tidal range. Researchers at the University of South Carolina and the Marine Biological Laboratory in Woods Hole have developed two coastal indicators that can be applied to assess the condition of coastal marshes (Morris et al., 2002; Morris, 2007). One is the vertical elevation relative to the mean sea level (geomorphic) and the other is the level of stress of marsh vegetation (physiologic). The following two sections provide examples of two indicators.

6.7.1.1 Geomorphic Indicator

The vertical elevation relative to the mean sea level is an important geomorphic indicator of marsh productivity and stability and is determined by using LIDAR remote sensing. This LIDAR elevation data is combined with a high resolution airborne data acquisition and registration (ADAR) digital camera image of the marsh landscape to construct a frequency distribution of marsh land cover with elevations relative to the elevation of the mean sea level. The frequency distribution is then compared to optimal distributions across the range of tolerance for the specific vegetation. The height of coastal marshes relative to the sea level moves upward or downward toward equilibrium with the sea depending on factors such as the rate of sea level rise and amount of sedimentation. When this equilibrium drops below an optimum level

either by a rapidly changing sea level or by changes in the supply of mineral sediment and organic matter, the salt marsh vitality declines. A decline in the relative elevation of the marsh surface below an optimum suggests that coastal marshes are on a course leading to degradation.

6.7.1.2 Physiological Indicator

The level of stress of marsh vegetation is an important indicator of marsh productivity and stability. Two complementary measurements, one ground based and the other remotely sensed, are applied to measure stress. One ground-based technique is based on the fluorescence emitted by a leaf as measured by a pulse-amplitude-modulated (PAM) fluorescence meter and gives an estimate of the efficiency of energy utilization by the leaf. A healthy leaf will have higher energy efficiency than a leaf that is stressed. The remotely sensed measurements detect different forms of xanthophyll pigments. Xanthophyll pigments change form in order to protect the plant's photosystems, so they can be used as an indicator of stress. The stress of marsh vegetation, as measured by the spectral reflectance of plant pigments, is governed by nutrient and water availability, phytotoxins, salinity, and the relative sea level. Combining marsh elevation data with measurements of the level of stress of vegetation is an integrative indicator of marsh productivity, health, and stability.

These indicators offer a cost-effective method for assessing the risk for wetland loss, as well as for monitoring the condition of coastal wetlands and the success of restoration efforts. Resource managers can use this information, for example, to apply mitigation techniques for adjusting the sediment supply for wetlands at high risk of inundation.

6.8 HUMAN IMPACTS AND MANAGEMENT OF COASTAL MARSHES

Human activity has impacted coastal marshes in many ways from direct destruction to environmental factors that affect marsh sustainability. One of the major ways in which coastal marshes have been impacted by human activity is by physical alterations that have led to the direct and indirect destruction of wetlands. A number of both natural and cultural factors lead to wetland loss, but in general, cultural factors have been more important. Wetlands along the US coast in areas with high population densities

TABLE 6.7 Rapid assessment types and possible outputs for different purposes

General Purpose	Biodiversity baseline		Disturbance and Ecosystem Health		Resource Use
Specific purposes	Baseline inventory; prioritization; conservation; identification	Conservation of specific species; status of alien species	Change detection	Overall ecosystem health or condition	Sustainable use of biological resources
Assessment type	Baseline inventory	Species-specific assessment	Change Assessment	Indicator assessment	Resource assessment
Types of data and analyses	1. Species lists/ inventories	1. Status of a focal species: distribution, abundance, population size/structure, genetic, health, size, species interactions, nesting, breeding and feeding information	1. Monitoring data	1. Data on health or condition of inland water systems	1. Presence, status and condition of economically, culturally, nutritionally, and socially important species
	2. Habitat type lists/ inventories	2. Ecological data on focal species; habitat, symbionts, predators, prey, etc.	2. Effects of an activity or disturbance on habitat/species/ communities: diversity loss, genetic issues, habitat changes or loss	2. Water quality data	2. Information on sustainable use of a species
	3. Limited data on population size/structure, community structure and function, and species interactions	3. Threats to focal species and habitats	3. Monitor impacts	3. Hydrological information.	3. Limited monitoring data: stock assessment data, habitat status.
	4. Abundances, distribution patterns, and ranges	4. Life history table	4. Determine changes in ecological character	4. Biological parameters	4. Limited information relevant to resource management
	5. Genetic information.	5. Water quality data	5. Impact reduction options	5. Biotic indices.	5. Water quality data
	6. Important species: threatened, endangered, endemics, migratory, invasive alien species, other significance: cultural, scientific, economic, nutritional, social	6. Hydrological information	6. Biotic indices		6. Hydrological information.
	7. Diversity indices		7. Habitat indices		
	8. Water quality data		8. Water quality data		
	9. Hydrological information		9. Hydrological information		
			10. Early warning indicators		

Source: From Secretariat of the Convention on Biological Diversity (2006).

have generally suffered the greatest proportional loss (Gosselink and Baumann, 1980), a reflection of the pressure of development in these areas. This is the case for most coastal areas globally. Wetlands have been drained, filled, and "reclaimed" in all parts of the world. In almost all coastal cities, large areas of wetlands have been destroyed for development of one kind or another. In many areas, the so-called "finger fill" developments have been constructed to allow boat access for homes and businesses.

Deltaic wetlands have been particularly impacted because deltas have largest areas of coastal wetlands, and deltas are used intensely for agricultural, industrial, urban, and navigation developments (Syvitski et al., 2009; Vörösmarty et al., 2009). The list of impacted deltas is long and includes the Rhine, Rhone, Ebro, Po, Nile, Mississippi, Colorado, San Joaquin-Sacramento, Tigris-Euphrates, Indus, Ganges, Mekong, and Yangtze. Only a few tropical (e.g., the Orinoco) and arctic (e.g., MacKinzie and Lena) deltas have remained relatively unaffected.

The Mississippi and Ebro Deltas serve as examples where human activities have resulted in dramatic regional changes in coastal systems. In the Ebro, the changes have proceeded deliberately for the most part to provide land for agriculture and water supply to other parts of Spain. In the Mississippi Delta, many of the changes have followed as a result of the indirect and cumulative impacts of human activities. In both cases, large areas of coastal ecosystems have been altered and destroyed.

The Ebro River basin (85,530 km^2) is located in Spain in the northeastern Iberian Peninsula and discharges to the western Mediterranean. Close to 190 dams, constructed mainly in the twentieth century, store approximately 60% of the annual runoff (about 11,859 hm^3/year). The water is used for hydroelectricity, but the main consumptive use is irrigation (6300 hm^3/year). Some 100 km upstream of the river mouth, two large dams (Mequinensa and Riba-roja) were constructed in the 1960s for hydropower. At 60 km upstream from the mouth, two channels were built in the late nineteenth century (total capacity of 50 m^3/s) for crop irrigation in the lower floodplain and delta.

The Ebro Delta (330 km^2) contains rice fields (210 km^2) and wetlands (80 km^2) and is rich in waterfowl and fisheries. The rice fields are in reclaimed wetlands. These habitats support important economic activities associated with tourism, hunting, fishing, and aquaculture. An extensive irrigation system delivers Ebro water to the rice fields, and therefore the wetland area has steadily decreased in the twentieth century due to conversion to agriculture and other uses. The creation of the Natural Park of the Ebro delta in 1983 protected much of the remaining wetlands, which occur in small areas near the beach and coastal lagoons.

Past and present management of the watershed have altered water, sediment, and nutrient fluxes of the lower Ebro River and its delta. Construction of the large dams reduced sediment transport to the lower Ebro River and delta by up to 99% (Ibáñez et al., 1996). Nearly half of the delta will be below sea level by 2100 due to subsidence, sea level rise, and sediment starvation. In addition, the shoreline is retreating several meters per year near the river mouth (Ibáñez, 2009).

Rising sea level will flood Mediterranean coastal wetlands gradually, unless enough sediment supply exists to offset the rise (Day et al., 1995; Ibáñez et al., 1997b, 2010; Pont et al., 2002; Day et al., 2011). Thus, some wetlands of the Ebro delta may disappear and rice fields are at risk due to increasing flooding and salt intrusion (Fig. 6.12). However, for deltas with high sediment loading, wetlands can survive sea level rise (Day et al., 1997). This stresses the importance of maintaining and restoring the sediment fluxes from the Ebro River to the sea that have been strongly reduced due to dam construction (Rovira and Ibáñez, 2007).

Proposed solutions to mitigate the impacts of climate change and relative sea level rise in the Ebro delta range from hard engineering methods (e.g., levees, dikes, and jetties) to soft engineering defenses (e.g., artificial dunes and drainage systems) and ecological engineering approaches (e.g., restoration of fluvial sediment fluxes, controlled diversions, and wetland restoration). These last approaches are the most sustainable in the long run, since the restoration of sediment delivery to the delta is the only solution to maintaining land elevation and wetland ecosystem integrity (Ibáñez, 2009; Sánchez-Arcilla et al., 2008). Preliminary studies (Rovira and Ibáñez, 2007) show that bypassing of sediments in the reservoirs of the lower Ebro river is feasible and represents a significant amount of sediments to offset the relative sea level rise in the delta plain and coastal retreat at the river mouth.

In the Mississippi Delta, dramatic changes have taken place, not because of deliberate planning, but because of the lack of it. Coastal wetland loss rates as high as 100 km^2/year occurred with a total loss of about 4500 km^2 or about 25% of the wetlands that existed at the beginning of the twentieth century (Fig. 6.13, Day et al., 2007). This was the result of a disastrous interaction of human actions and natural processes. The Mississippi Delta, like all deltas, was

Increasing soil salinity affecting crops

Urban areas at risk

Decreasing river flow and sediments

Land subsidence of 3 mm/year

Coastal retreat of 10 m/year

Sea-level rise of 3 mm/year

Summer hypoxia and mussel mortality

Bay $T°$ up to 30 °C in summer

Image NASA
Image © 2007 DigitalGlobe
Image © 2007 Institut Cartogràfic de Catalunya
© 2007 Cnes/Spot Image

Google

Pointer 40°39'49.79" N   0°44'24.52" E   elev   1 m Streaming |||||||||| 100%   Eye alt   32.96 km

FIGURE 6.12   Overview of the combined impacts of climate change, sediment deficit, and decreased runoff, presently existing in the Ebro Delta (Catalonia, Spain). *Source*: From Ibáñez (2009).

formed by the successive building of a number of major delta lobes as the river changed course every 500–1000 years (Roberts, 1997). The entire deltaic region is subsiding at a rate of about 1 cm/year because of such processes as compaction, consolidation, and dewatering of sediments deposited by the river. The sinking due to subsidence and rising sea level causes a high rate of relative sea level rise. In order to survive, wetlands must grow upward at the same rate as the water level rise. If not, they will be stressed by excessive flooding and other stresses and will ultimately die, as described earlier in this chapter. Historically, seasonal flooding by the Mississippi River into coastal marshes without extensive alterations of hydrology allowed coastal marshes to survive.

A number of human impacts have altered the natural cycle in the delta. One of the most important is that the river has been diked essentially to its mouth. Thus riverine input has ceased for most of the coastal zone. The wetlands themselves have also been altered dramatically. Large areas have been impounded (Day et al., 1990) and earlier impoundments were reclaimed for agriculture, but these projects mostly failed owing to subsidence due to organic soil oxidation. Most can be identified today as large rectangular water bodies

in the coastal marshes. A very damaging impact in the wetlands has been the construction of over 15,000 km of canals for drainage and navigation, mainly for petroleum exploration and production. These canals destroy wetlands directly, but cumulatively they have led to changes in the regional hydrology and salt water intrusion (Shaffer et al., 2009). Finally, the spoil banks that border these canals are barriers to overland sheet flow of water and they alter wetland hydrology (Swenson and Turner, 1987). Thus, the spoil banks impede water exchange, sediment deposition, and movement of nekton. Since sediments resuspended by winds are important for marsh surface accretion, canals with associated spoil banks are important factors contributing to land loss. It is clear that, unless action is taken to reintroduce riverine sediments and restore hydrology, most of the wetlands of the Mississippi Delta will disappear within this century (Reyes et al., 2000; Day et al., 2007). Indeed, Blum and Roberts (2009) recently concluded that the combination of sea level rise and sediment starvation would result in the almost complete loss of coastal wetlands in the Mississippi delta by 2100. We address issues of restoration and management of the Mississippi delta further in Chapter 19 and the impacts of climate change on the delta in Chapter 20.
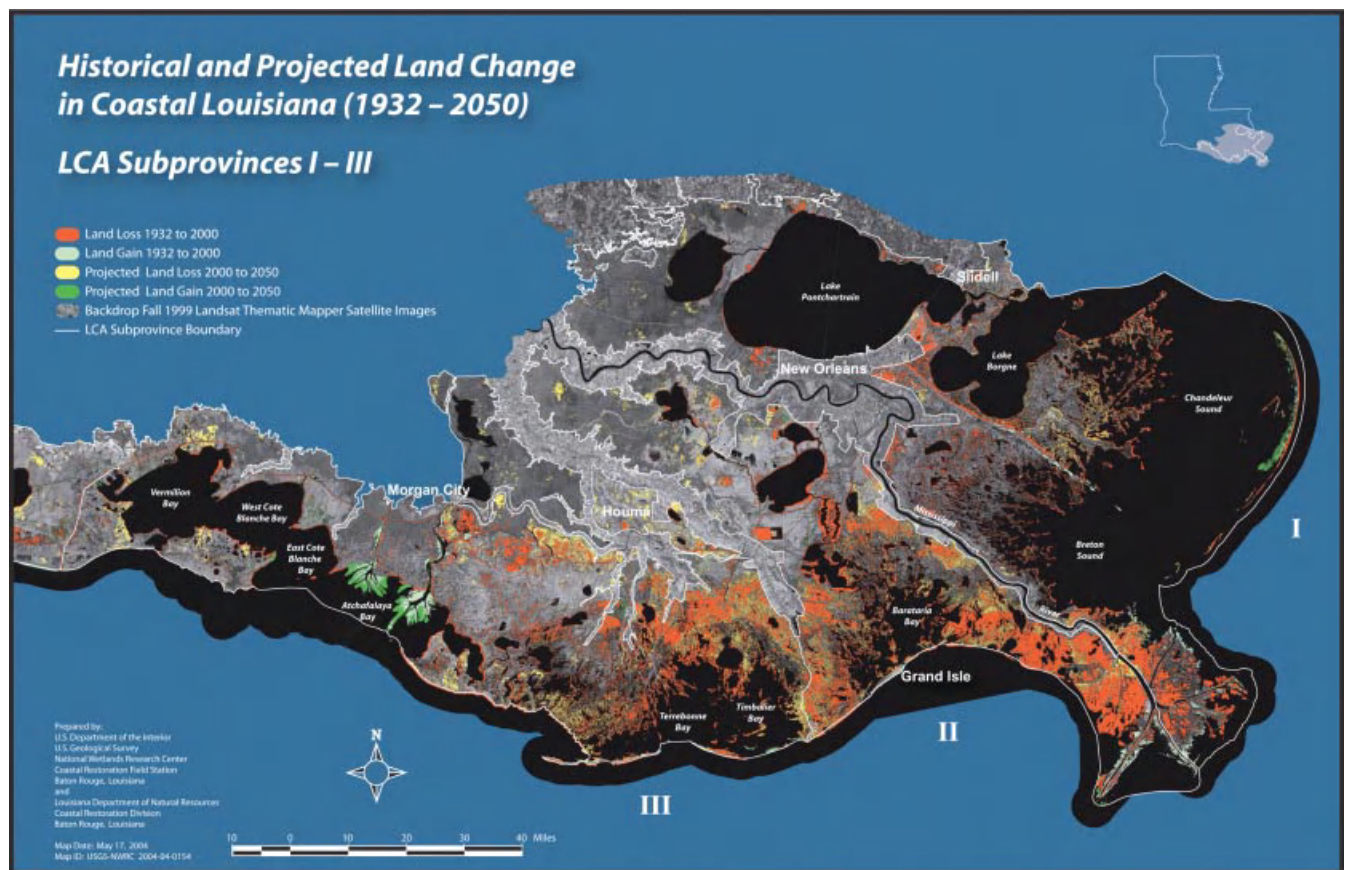
FIGURE 6.13 Wetland loss in the Mississippi delta.

Human activities have resulted in large coastal areas going below sea level. The sinking of coastal wetlands can be due to oxidation of organic soils after drainage or the extraction of belowground liquids or natural gas. Drainage of highly organic wetland soils in the metropolitan New Orleans area created parts of the city that are 4–5 m below sea level and 60–80% of the population living below sea level. Extraction of oil and gas in the Mississippi delta in some cases has doubled the rate of wetland subsidence (Morton et al., 2002; Ko and Day, 2004). Other areas have been similarly affected. For instance, most of the Sacramento-San Joaquin is below sea level due to oxidation of drained organic soils, whereas in the Po delta (Italy), extraction of shallow deposits of natural gas has caused parts of the delta to subside 3–4 m below sea level (Sestini, 1992).

6.8.1 Upstream Alterations

Upstream changes in rivers can have pronounced effects on coastal wetlands (Sklar and Browder, 1998). Two of the most important impacts are reduced freshwater discharge and reduced mineral sediment input. Construction of dams has resulted in the diversion of freshwater upstream for irrigation and for industrial and residential use. On the other hand, channelization of streams causes more rapid pulses of water to coastal systems. Construction of impoundments on the Mississippi River system has resulted in about a 50% decrease in suspended load (Meade and Parker, 1984; Blum and Roberts, 2009). Freshwater diversions from the Colorado River in the western United States are causing hypersaline conditions and deterioration of the delta of the river at the northern extent of the Gulf of California. Because most of the water use occurs in the United States but the coastal problems are felt in Mexico, this issue has been an important point of contention and discussion between the two countries. Salinization is particularly a problem in arid and semiarid areas where freshwater input has been reduced. For example, large freshwater withdrawals from the Indus River have led to hypersaline soils and loss of tens of thousand of hectares of wetlands in the Indus delta (Snedaker, 1984). As indicated above, freshwater and suspended sediments have been reduced by more than 90% in the Ebro, resulting in parts of the delta sinking below sea level (Ibáñez et al., 1996, 1997b).

The construction of the Aswan High Dam is an excellent case study of the impact of dam construction on a coastal wetland ecosystem (Stanley, 1996). Because of the loss of sediments, the shoreline of the Nile delta is now undergoing retreat. Stanley (1988) reported that the eastern part of the delta was undergoing subsidence of about 0.5 cm/year. This rapid subsidence combined with reduction of sediment and freshwater input due to the Aswan Dam and rising sea level is likely to lead to flooding and salinization of a large part of the delta plain by the end of next century (Milliman et al., 1989). Because the Nile delta is the site of most food production in Egypt, this will have a strong societal impact in this century.

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MANGROVE WETLANDS

Robert R. Twilley and John W. Day Jr.

7.1 BIOGEOGRAPHY AND ADAPTATIONS

Mangroves refer to a unique group of wetlands that are dominated mainly by trees that colonize the intertidal zone of tropical and subtropical coastal landscapes (Fig. 7.1), generally between 25° N and 25° S latitude (Lugo and Snedaker, 1974; Tomlinson, 1986; Duke et al., 1998). Early definitions of mangroves included the plant community dominated by trees in tropical coastal zones below the high tide mark, and the term *tidal forest* is a common synonym for mangrove forest. Other species occurring in mangrove swamps include vegetation such as shrubs, palm, and ground fern that occur in only part of the intertidal zone and adapted to salty water (Duke et al., 1998). True mangrove trees can be defined based on five unique characteristics: (i) complete fidelity to the intertidal zone (do not occur in terrestrial environments); (ii) taxonomic isolation from terrestrial relatives, at least to the generic level; (iii) community composition that commonly forms pure stands; (iv) morphological specialization representing adaptation to intertidal environment including aerial roots, and vivipary of embryo; and (v) physiological adaptations including salt exclusion, salt secretion, and salt accumulation (Tomlinson, 1986). Trees with these characteristics are called *true mangroves*.

The term *mangrove* may best define a specific type of tree, whereas *mangrove wetland* refers to the whole plant associations with other community assemblages in the intertidal zone (Duke et al., 1998), similar to the term *mangal* introduced by Macnae (1968) to refer to tropical, coastal swamp ecosystems. These are important distinctions since the biodiversity of mangroves may be considered species poor in some regions if only the tree species richness is considered, but the biodiversity of mangrove wetlands, including all the flora and fauna, may equal that of the other tropical ecosystems (Rüetzler and Feller, 1996; Twilley et al., 1996). In addition, the habitats of tropical estuaries are diverse, consisting of a variety of primary producers and secondary consumers distributed in bays and lagoons in which the intertidal zone is dominated by mangrove wetlands. These may be referred to as *mangrove-dominated estuaries*. Thus there is a hierarchical use of the term mangrove that can be used to describe individual trees, to tropical, coastal forested wetland ecosystems, and even tropical estuarine landscapes. In this chapter, the focus is on the ecological characteristics of mangrove wetlands by describing individual, community, and ecosystem features of landscapes dominated by these unique wetland plants.

7.1.1 Global Patterns

Mangroves are a group of halophytes with species from 28 genera in 20 different families and two plant divisions with approximately 52 species recognized throughout the world (Duke et al., 1998; Table 7.1 and Fig. 7.2). There are 17 species that have been described as exclusively mangroves (true mangroves described

TABLE 7.1 World occurrence of mangrove taxa in six global biogeographic regions (Fig. 7.2), common estuarine and intertidal distributions (from Duke, 1992), with brief descriptions of structure and dispersal mechanism (based on Tomlinson, 1986). Table is modified from Duke et al. 1998

Genus	Species	Structural Character			Global biogeographic regions						Estuary Location			Intertidal Position			Dispersal
		Form	Can	AGR	A	E	P	I	W	P	D	I	U	L	M	H	
Acanthus	ebracteatus	S	U	-					5	6		I	U		M	H	Seeds
	ilicifolius	S	U	-					5	6		I	U		M	H	Seeds
Acrostichum	aureum	F	U	-	1	2	3	4	5	6		I				H	Paraphyses
	danaeifolium	F	U	-	1	2				6			U			H	Paraphyses
	speciosum	F	U-C	-					5	6		I	U			H	Paraphyses
Aegialitis	annulata	S	U-C	-					5	6	D				M	H	Hypocotyl
	rotundifolia	S	U-C	-					5			?			?		Hypocotyl
Aegiceras	corniculatum	S	C	-					5	6		I	U	L		H	Hypocotyl
	floridum	S	C	-					5			?			?		Hypocotyl
Aglaia	cucullata	T	C	P					5			I	U		M		Seeds
Avicennia	alba	T	C	P					5	6	D	I	U	L	M		Cotyledon
	bicolor	T	C	P	1					6	D					H	Cotyledon
	germinans	T	C	P	1	2	3				D				M	H	Cotyledon
	integra	T	C	P-r						6		I		L			Cotyledon
	marina	S/T	C	P	+1			4	5	6	D	I		L	M	H	Cotyledon
	officinalis	T	C	P					5	6		I		L			Cotyledon
	rumphiana	T	C	P													
	schaueriana	T	C	P		2					D	I			M	H	Cotyledon
Brugiuera	cylindrica	T	C	B-k					5	6	D	I			M	H	Hypocotyl
	exasistata	S/T	C	B-K						6	D	I	U			H	Hypocotyl
	gymnorrhiza	T	C	B-K				4	5	6	D	I			M	H	Hypocotyl
	hainesii	T	C	B-K					5	6		I				H	Hypocotyl
	parviflora	T	C	B-K					5	6	D	I			M	H	Hypocotyl
	sexangula	T	C	B-K					5	6		I	U		M	H	Hypocotyl
Camptostemon	philippensis	T	C	-					5	6		?			M	H	Hypocotyl
	schultzii	T	C	-						6	D	I		L	M	H	Hypocotyl
Ceriops	australis	S/T	C	B					5	6	D	I			M	H	Hypocotyl
	decandra	S/T	U-C	B					5	6		I			M	H	Hypocotyl
	tagal	S/T	C	B				4	5	6	D	I			M	H	Hypocotyl
Conocarpus	erectus	S/T	C	-	1	2	3		5	6	D	I				H	Capsule
Cynometra	iripa	S	U	-						6		I	U			H	Capsule
Diospyros	littoralis	T	C	-						6		I	U		M	H	Seed
Dolichandrone	spathacea	T	C	-						6			U		M	H	Seeds
Excoecaria	agallocha	T	C	K				4?	5	6	D	I	U		M	H	Seeds
	indica	T	C	K					5		D	I	U	L	M		Seeds
Heritiera	fomes	T	C	B					5				U			H	Capsule Closed
	globosa	T	C	B					5				U			H	Capsule Closed
	littoralis	T	C	B				4	5	6		I				H	Capsule Closed
Kandelia	candel	S/T	C	B				4	5		D			K			Hypocotyl

Genus	species	Form	Can	AGR	1	2	3	4	5	6	D	I	U	L	M	H	Propagule
Laguncularia	racemosa	S/T	C	k	1	2	3				D	I			M	H	Hypocotyl
Lumnitzera	littorea	S/T	C	k					5	6		I				H	Hypocotyl
	racemosa	S/T	C	k				4	5	6	D				M	H	Hypocotyl
	x rosea	S	C	k					5?	6	D				M	H	Capsule Closed
Mora	oleifera	T	C	B	1						I					H	Husk intact
Nypa	fruticans	P	C	-		+2	+3		5	6			U	L	M	H	Seed
Osbornia	octodonta	S/T	C	-					5	6	D		U		M	H	Pericarp intact
Pelliciera	rhizophoriae	T	U-C	B	1	2					D		U		M	H	Seeds
Pemphis	acidula	S	C	-				4	5	6	D				M	H	Seeds
Rhizophora	apiculata	T	C	R					5	6	D	I		L	M		Hypocotyl
	mangle	S/T	C	R	1	2	3				D			L	M		Hypocotyl
	mucronata	T	C	R				4	5	6		I	U	L	M		Hypocotyl
	racemosa	T	C	R	1	2	3					I		L	M		Hypocotyl
	samoensis	T	C	R						6	D			L	M		Hypocotyl
	stylosa	S/T	C	R					5	6	D			L	M		Hypocotyl
	x harrisonii	T	C	R	1	2	3				D	?		L	?		Hypocotyl
	x lamarckii	T	C	R					5	6	D	I		L	M		Hypocotyl
	x selala	T	C	R						6	?				?		Hypocotyl
Scyphiphora	hydrophyllacea	S	U-C	-					5	6		I				H	Calyx intact
Sonneratia	alba	T	C	P				4	5	6	D			L	M		Seeds
	apetala	T	C	P					5				U	L			Seeds
	caseolaris	T	C	P					5	6			U	L	M		Seeds
	griffithii	T	C	P					5		D			L			Seeds
	lanceolata	T	C	P					5	6			U	L			Seeds
	ovate	T	C	P					5	6	D				M	H	Seeds
	xgulngai	T	C	P					5	6		I		L	M		Seeds
	x urama	T	C	P					5?	6		I			M		Seeds
	alba x ovate	T	C	P					5		?				?		Seeds
Tabebuia	palustris	S	U	-	1								U		M		Seeds
Xylocarpus	granatum	T	C	B				4	5	6		I		L	M	H	Seeds-tetrahedral
	mekongensis	T	C	K-P					5	6		I			M	H	Seeds-tetrahedral

Life form (Form): T = tree; S = shrub; P = palm; F = ground fen. Global regions: 1 = W. America; 2 = E. America; 3 = W. Africa; 4 = E. Africa; 5 = Indo-Malesia; 6 = Australasia; + = introduced. Canopy position (Can): C = canopy; U = under canopy; I = intermediate (lower case = diminutive form). Above-ground roots (AGR): R = prop roots; P = pneumatophores; B = buttresses; K = knee roots (lower case = diminutive form). Upriver location: D = downstream; I = intermediate; U = upstream. Tidal (above Mean Sea Level) position: L = low intertidal; M = medium intertidal; H = high intertidal.

FIGURE 7.1 (a) Fringe mangrove along Shark River slough dominated by *Rhizophora mangle*. (b) Interior mangrove forest in Puerto Rico dominated by *Avicennia germinans*. (c) Fringe mangrove in carbonate islands off coast of Belize dominated by *R. mangle* with sea grasses in the subtidal zone. (d) Riverine mangrove forest along Guayas River estuary in Ecuador dominated by *Rhizophora harrisonii*.

above). A total of 36 species have been described from the Indo-West Pacific area, but fewer than 10 species are found in the new world (Macnae, 1968) reflecting the old world origin of mangroves (Fig. 7.2). In addition, there is a strong effect of latitude on species richness in the eastern hemisphere with maximum richness along the Equator (40 species) and reduction by half at 20° north and south latitude (Ellison et al., 1999). The Gulf of Mexico and Caribbean have even lower species richness with only four mangroves commonly found in the region including red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*). *Rhizophora* (Rhizophoraceae) and *Avicennia* (Avicenniaceae) have

eight species each, representing the most diverse genera of mangrove trees, and each has about five species in the old world compared to three in the new world tropics (Table 7.1). There are three other genera in the Rhizophoraceae family, all of which are located only in the old world tropics (*Bruguiera* has six species, all in the old world tropics). The other dominant contribution of species to old world tropics is *Sonneratia* (Sonneratiaceae), which has five species. In addition, most of the minor components that are relatively rare of mangroves are located in the old world tropics (nearly 19 species), with only one, *Pelliciera*, located in the new world tropics (Tomlinson, 1986; Duke et al., 1998; Ellison et al., 1999).
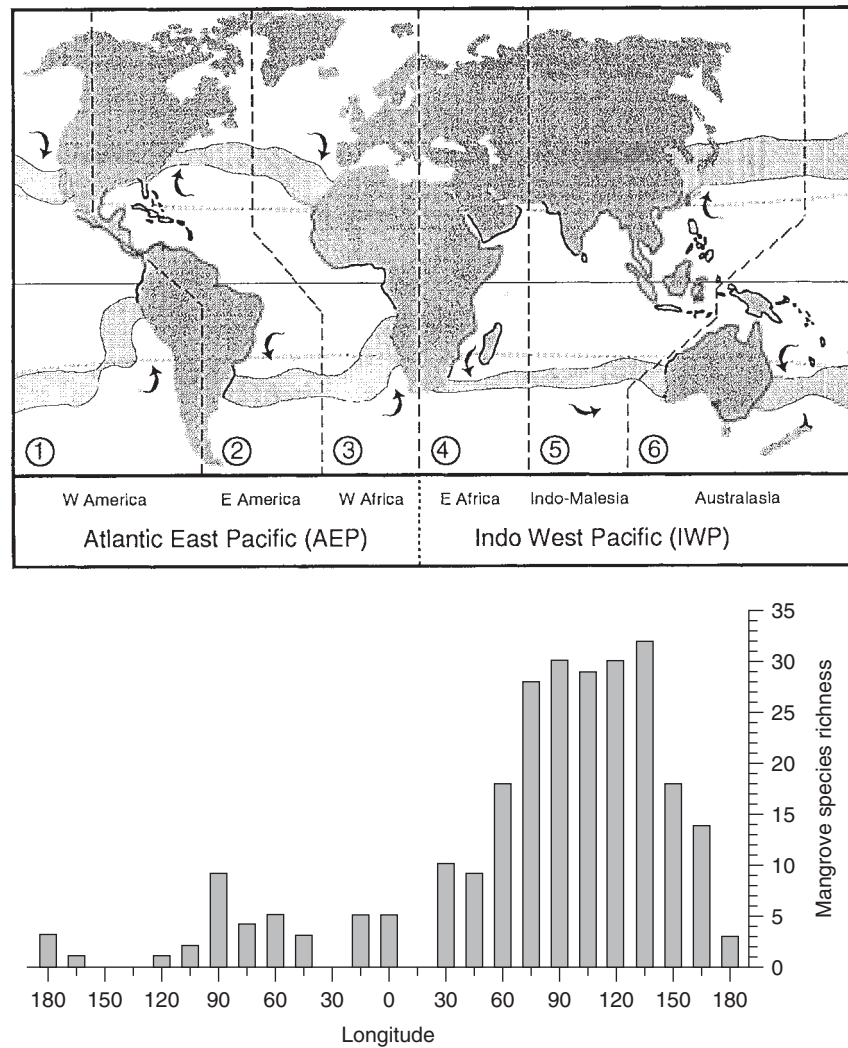
FIGURE 7.2 Global distribution of mangroves based on Duke et al. (1998) in upper panel and Ellison et al. (1999) in lower panel.

There are clear patterns in tree richness of mangrove wetlands between the eastern and western hemispheres, but the total mangrove wetland area in the coastal zone of these two regions is very similar (Fig. 7.2; Ellison et al., 1999). There is an estimated 170,000 km^2 of mangrove wetlands worldwide, with about 75% of that total found between $0°$ and $10°$ north and south latitude of the Equator. Thus, both species richness and mangrove distribution are high near the Equator. About 77,169 km^2 located in Asia, which along with Australia to the south (10,287 km^2), makes up over half of the global mangrove area. The most extensive region of mangrove wetlands in the new world tropics is located along the coast of Brazil, followed by Mexico and Venezuela. The most extensive areas of mangrove wetlands are in coastal environments with muddy coasts and reduced

disturbance from cyclones or strong winds that can limit the development of old growth forests.

The distribution and abundance of mangrove wetlands is also most extensive along shores where the average air temperature of the coldest month is higher than $20°C$ and where the seasonal range does not exceed $10°C$ (Walsh, 1974; Chapman, 1976). The global distribution of mangroves (Fig. 7.2), particularly in the northern and southern limits, appears to correlate reasonably well with the $16°C$ isotherm for the air temperature of the coldest month (Chapman, 1976). Northernmost populations occur at $32°$ N latitude (Bermuda and Japan), and southernmost populations occur at $37–38°$ S latitude (Australia and New Zealand; Krauss et al., 2008). The frequency, duration, and/or severity of freezing temperature are the prime factors governing the distribution and abundance of

mangroves in the upper subtropical zones (Lugo and Patterson-Zucca, 1977; Sherrod et al., 1986; Kao et al., 2004; Stevens et al., 2006; Stuart et al., 2007).

The greater resprouting ability of *Avicennia* (black mangrove, Fig. 7.1b) and *Laguncularia* (white mangrove) mangroves results in greater recovery from freeze damage (Lugo and Patterson-Zucca, 1977). Black and white mangroves have extensive secondary meristematic tissues and can quickly recover by developing sprouts following defoliation of the canopy (Snedaker et al., 1992). Impacts on the physiological effects of chilling and freezing temperatures on plants include the following in the order of most severe effects: (i) increase the rigidity of biomembranes and increase the energy required for activating biochemical reactions; (ii) cause chilling injury (as a consequence of lesions in biomembranes and interruption of energy supply to cells); and (iii) freeze plant tissues, leading to vascular embolism, dehydration, or cellular rupture. The lower threshold temperature range for tropical trees including mangroves (leaf tissue) is $+5$ to $-8\,^{\circ}\text{C}$ (Larcher, 2001; Krauss et al., 2008).

7.1.2 Vivipary

Vivipary is the condition whereby the embryo (the young plant within the seed) grows first to break through the seed coat and then out of the fruit wall while still attached to the parent plant (Fig. 7.3). This condition is common among mangrove trees and can be found in the species of the genera *Bruguiera, Ceriops, Kandelia*, and *Rhizophora. Cryptovivipary* (Greek kryptos, hidden) refers to the condition whereby the embryo grows to break through the seed coat but not the fruit wall before it splits open. This condition is exhibited in *Aegiceras, Avicennia*, and *Nypa* species. Vivipary, including cryptovivipary, is a rare phenomenon among higher plants, occurring mostly among plants of tropical shallow marine habitats, such as sea grasses (20 genera in 13 families) and mangroves (7 families). The storage material of large propagules provides nutrition during the early stages of development. Accumulation of starch within the hypocotyls mean that rooting, erection of the propagule in the vertical position, and respiration and growth can take place initially without being limited by nutrition from photosynthesis. Early growth in mangrove seedlings is linked to maternal reserves (Ellison and Farnsworth, 1993; Ball, 2002) and their strategies to capture and utilize soil resources and light (McKee, 1995a, 1995b). Therefore, seedling responses to environmental and biotic factors determine the success of its conversion to the adult phase (Bazzaz, 1990). The transport of propagules with tides
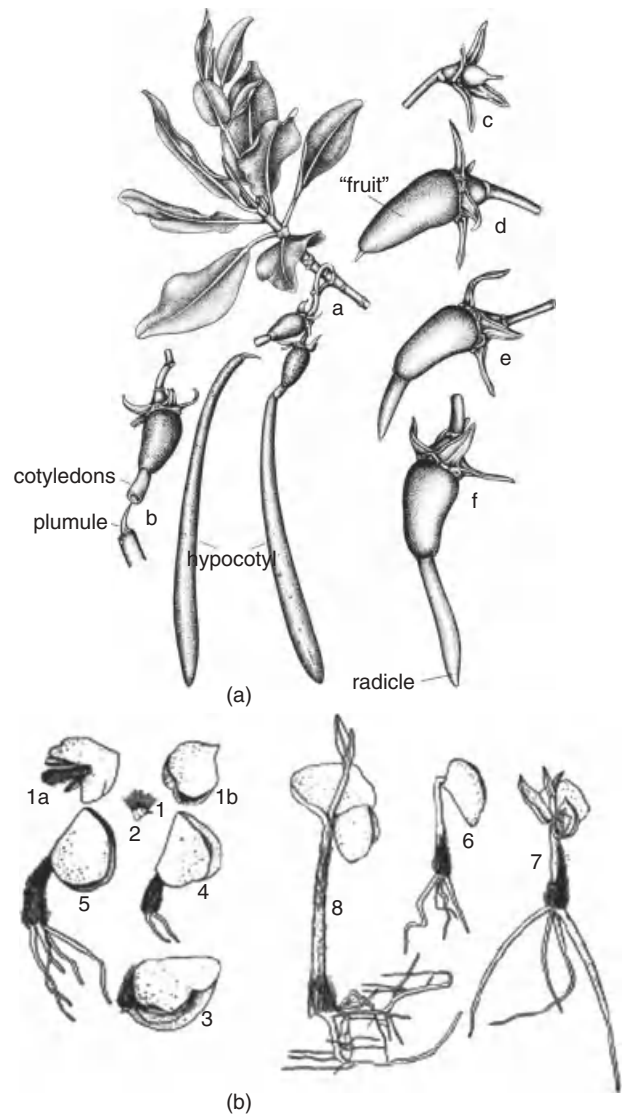
FIGURE 7.3 (a) Seedling development showing viviparity of *Rhizophora mangle* and (b) cryptoparity of *Avicennia germinans* (Panel A is from Tomlinson 1986 and Panel B is from Chapman 1976)

has been cited as a critical dispersal mechanism that favors living in coastal intertidal zones.

7.1.3 Hydroperiod and Waterlogged Soils

Hydroperiod is associated with the frequency and duration of flooding, which can be described in specific inundation classes of mangroves and impoundments (Watson, 1928; Chapman, 1944; McKee and Mendelssohn, 1987). These inundation classes explain that hydroperiod establishes patterns of zonation that control seedling establishment and growth in mangroves. In Malaysia, five inundation classes described the distribution patterns of 17 mangrove species,

ranging from inundation by all high tides to inundation by only spring tides. Nearly 50% of Malaysian mangroves were included in a lower inundation class, defined as two or fewer inundations per month associated with exceptional or equinoctial tide. Chapman (1976), who applied Watson's categories to south Florida mangroves, indicated that *R. mangle, A. germinans, L. racemosa*, and *C. erectus* transgress the inundation continuum from the wettest to driest. All three species are present in sites flooded from 30% to 50% of a year. Actual inundation durations between 50% and 75% often result in populations of *R. mangle*, while *L. racemosa* and *A. germinans* are generally restricted to durations less than 50% (Krauss et al., 2006).

Muddy intertidal environments also require the plants to adapt to waterlogged soils that are not only anaerobic but may also contain elevated levels of sulfide and other reduced minerals. Mangroves are known for adventitious roots that provide morphological adaptations to lack of oxygen in muddy soils (Fig. 7.5b). Most mangrove species have a shallow cable root system, within 2-m depth, that spreads away from the tree trunk. Attached to this horizontal root system are vertically descending anchor roots, which have attached, fine nutritive roots. There are five types of aboveground root adaptations (Fig. 7.5b): (i) pneumatophores are the conical projections extending vertically upward from the cable root system, extending above the ground at a height proportional to average flooding depths; (ii) knee roots grow aboveground and then back down into sediment; (iii) stilt or prop roots branch from the main tree trunk, extending downward to soil surface forming fine roots in the soil; (iv) buttress roots are the bladelike structures, as modifications of lower tree trunk; and (v) aerial roots are the stilt roots from tree trunks and branches that extend downward but do not attach to the soil (Saenger, 2002).

Nearly, all of these roots have specialized cells, called *lenticels*, which allow the passage of oxygen to internal tissue and fine roots in otherwise anaerobic environments. Physiological adaptations of roots include ethylene accumulation, which promotes adventitious root production, and tannins that might reduce phytotoxic effects of reduced iron and sulfides in the soil solution as well as sequestration of dissolved organic nitrogen (Delaune and Reddy, 2008). In addition, metabolic adaptations allow mangroves to avoid accumulation of ethanol under anaerobic conditions; rather malic acid is the end product of anaerobic respiration, which is less toxic and involved in ionic balance and salt uptake. These mechanisms allow mangrove roots to survive both external (soil) and internal (root) toxic conditions of living in anaerobic soils.

The level of stressed conditions in mangrove soil is linked to the duration of flooding and thus the degree of anaerobic environment. A primary determinant of the biochemical processes in mangrove soils is the relative distribution of oxidation and reduction zones that are dependent on the presence of dissolved oxygen. The upper oxidation zone in mangrove soils is controlled by the limit that atmospheric oxygen is diffused to pores of dry (0.205 cm^2/s in air) versus wet (0.227×10^{-6} cm^2/s in water) soils. In addition, the normally high concentration of organic matter in mangrove soils, due to both litter and root productivity, establishes high sediment oxygen demand. Several mechanisms can enhance oxygen supply by increasing diffusion into otherwise oxygen-deficient soils (Clark et al., 1998) including (i) sediment texture, which dictates porosity, and permeability that controls diffusive flux (Hutchings and Saenger, 1987); (ii) position of the water table, which may vary seasonally with hydroperiod (balance of tides and rain events; Twilley and Chen, 1998); and (iii) influence of biota (directly and indirectly) on water and oxygen exchange with sediments (Thongtham and Kristensen, 2003; Kristensen, 2008).

When the dissolved oxygen necessary to supply aerobic respiration is absent, there are a series of alternate electron acceptors used by anaerobic microbes in the soil to terminate electron flow during respiration (respiration is the oxidation of organic matter and reduction of electron acceptors). When oxygen is present, it is reduced to water as electrons are exchanged with organic matter forming energy. The collection of electrons by reactants in the absence of oxygen results in the following transformations under reduced conditions: manganese (Mn^{3+}) and iron (Fe^{3+}) are reduced to Mn^{2+} and Fe^{2+}, respectively, NO_3^- is reduced to N_2 or N_2O, SO_4^{2-} is reduced to sulfide (S^{2-}), and CO_2 is reduced to methane (CH_4). Since sulfate is normally the most abundant electron acceptor in the absence of oxygen in most mangrove soils (because of the presence of seawater), the "reduction zones" are characterized by the presence of decomposing organic matter and substantial populations of sulfate-reducing bacteria that produce sulfides. Landscape gradients in hydroperiod establish the depth that oxygen diffuses into surface sediments, particularly in seasonally dry forests. Below the surface of the water table, the soil zone is reduced leading to an oxidized zone above the reduced zone in these dry conditions. During the wet season, water fills these pore spaces, forming strong
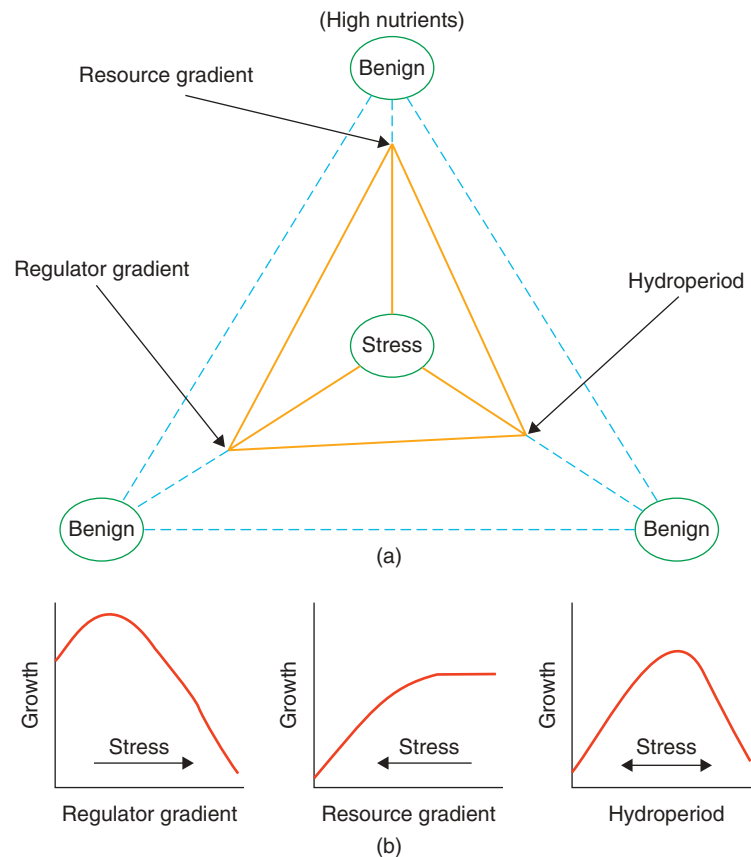
FIGURE 7.4 Factorial interactions controlling the productivity of coastal wetlands including regulators gradients, resource gradients, and hydroperiod. *Source:* From Twilley and Rivera-Monroy (2005).

seasonal shifts between wet and dry seasons from oxidized to reduced zones as the lower reduction zone migrates to the soil surface. The relative distribution of reduction zones produces by-products of anoxic respiration including HS^- and H^+ ions that both regulate plant growth. Even under completely reduced condition within soil columns, there are microsites of oxidized zones formed by the release of oxygen from roots. These oxygen microsites around finer roots can limit the toxic effects of substances formed by anaerobic by-products. This is an adaptation of mangroves to surviving in anaerobic waterlogged conditions (Twilley and Rivera-Monroy 2009).

7.1.4 Resources and Regulators

Mangrove distribution in the intertidal zone is determined by a variety of stress conditions (Fig. 7.4) that can be grouped into three categories: resources, regulators, and hydroperiod (Twilley and Rivera-Monroy, 2005). Resources include attributes of the environments such as light, water, nutrients, and space that meet two requirements: they are (i) essential to tree growth and (ii) consumed by trees during growth

thus reducing the availability of this resource to be used by neighbors (Huston, 1994). This latter condition establishes competition for resources and thus more complex ecological interactions in the intertidal zone. Regulators also influence plant growth, such as salinity, sulfide, pH, and temperature, but are not consumed during the growth process and thus there is no change in regulator condition because of plant response (Tilman, 1982). The third category, hydroperiod, is the frequency, duration, and depth of water inundation (tide and precipitation) that can control wetland growth (Gosselink and Turner, 1978). It could be argued that hydroperiod is a regulator, an attribute that controls growth but is not consumed, but this is specifically included as a unique category since it can dominate the concentration and availability of resources and regulators in wetland environments. As described above, the distinction in resources and regulators is that while both influence plant growth, the consumption of resources during plant growth can establish competition among plants (within and among species) as the resource concentration decreases with increased growth (assuming
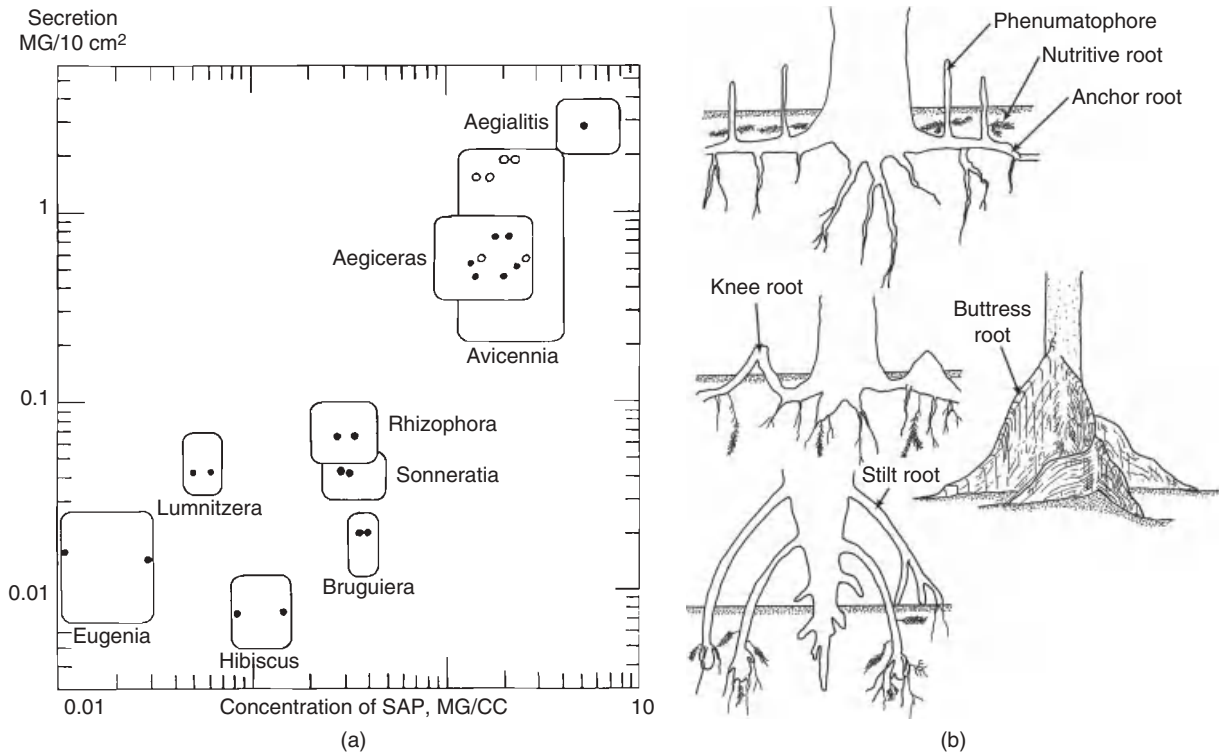
FIGURE 7.5 Adaptations of mangroves to intertidal environment. (a) Salt excretion rates for mangrove species (Tomlinson, 1986). (b) Adaptations of root structures to anaerobic environments (Saenger, 2002).

no new supply). Mangrove wetlands inhabit stressed tropical coastal environments (Lugo, 1980), where each tree species has adaptations to specific tolerances within the intertidal zone in response to conditions of resources, regulators, and hydroperiod (Fig. 7.4).

One of the most critical regulators controlling propagule establishment, seedling survival, and plant growth is salinity (Scholander et al., 1962; Chapman, 1976; Tomlinson, 1986; Ball, 1988a, 1988b; Chen and Twilley, 1998; Krauss et al., 2008). Living in the marine environment requires special adaptation to water balance imposed by the presence of salt that results in many adaptations similar to plants that live in xeromorphic (dry) conditions. Trees particularly require more specialized capacity to translocate water from the soil to the canopy at tens of meters above the soil surface. To move water up a tree to a leaf in the canopy, the water potential in the plant must be more negative than the saline water around plant roots. For a tree in freshwater, water potential is zero and water potentials in leaves are around -30 atm (range from -26.6 to -56.3 atm). However, in normal saline water, osmotic potential may be -30 atm, so that the water potential in the canopy of a mangrove must be more negative to transport water to the leaf surface. There are several mechanisms that

are common among halophytes (Chapter 6) such as salt exclusion, salt secretion, salt storage, succulence, ion compartmentalization, and osmo-compensation. There are also special metabolic adaptations that promote nitrogen metabolism, protein synthesis, purine nucleotide synthesis, carboxylation enzyme inhibition, and reduced stomatal conductance. Mangroves have many of these morphological and physiological adaptations that are thought to conserve water at both the leaf level (Ball, 1988a) and the individual tree level (Krauss et al., 2008).

Salt glands are a special adaptation of mangroves that allow for secretion of salt from mangrove leaves (Fig. 7.5a). This adaptation varies among mangrove species and is higher in *Avicennia* and *Aegiceras* when compared to *Rhizophora, Sonneratia*, and *Bruguiera* (Scholander et al., 1962). This capacity in salt secretion occurs more frequently in plants that dominate community composition of mangrove wetlands in more interior zones that are more distant from shoreline where higher salt content occurs in soil waters. As discussed in Section 7.2.1, the more interior region of the intertidal zone is where salt accumulates in soil requiring special adaptations to hypersaline conditions.

Hypersaline soils are also sites where mangroves have adaptations associated with the exchange of water and CO_2 through specialized openings on leaf surface, called *stomata*, that control the delicate balance of water loss by evapotranspiration and carbon gain by photosynthesis. Low stomatal conductance, which reduces exchange of gases through these openings in the leaf, is also a characteristic of salinity strategy as freshwater loss through stomata is balanced against limited CO_2 gain (Ball and Farquhar, 1984). Species that are more tolerant to higher salinity are typically more efficient in water use as described by the amount of carbon gain through stomata compared to the amount of water lost (Ball, 1996). Given these constraints on water loss and carbon gain in soils with saline conditions, optimum photosynthesis of mangroves has been documented at about 17% of full strength seawater, or about 6 psu salinity. The salinity that represents the upper limit of photosynthesis varies among mangrove species resulting in one of the parameters that controls plant zonation along the intertidal zone (described below). *Avicennia, Aegialitis, Excoecaria*, and *Laguncularia* all have tolerance (based on field observations) above 85 psu (Tomlinson, 1986); however, *Laguncularia* is considered less tolerant based on several updated studies (Krauss et al., 2008).

Another regulator in the intertidal zone is hydrogen sulfide (McKee et al., 1988; McKee, 1993, 1995a). Greenhouse experiments show differential tolerance of mangrove seedlings to flooding (Cardona-Olarte et al., 2006; Krauss et al., 2006). Yet, field experiments also show that adult mangrove plants can grow in soils with high concentration of sulfide such as 3.75 mmol/l for *A. germinans* (Nickerson and Thibodeau, 1985), 1.63 mmol/l for *R. mangle* and 1.44 mmol/l for *A. germinans* (Mckee et al., 1988), and 3 mmol/l for *A. germinans* and 1.7 mmol/l for *R. mangle* (McKee, 1993). There are mechanisms that can reduce the harmful effects of hydrogen sulfide by binding the sulfide to a mineral, thus eliminating its toxic effect. One key mechanism is the release of dissolved oxygen from roots, and chemical binding of hydrogen sulfide with species of reduced iron, forming compounds that are considered nontoxic to mangroves. There is evidence across many genera of mangroves that different root systems have capability of releasing oxygen and is thus a strategy that permits plants to survive waterlogged soils that accumulate hydrogen sulfide.

In the absence of significant control of plant growth by regulators in the intertidal zone, resources can set the rate of net primary productivity. Light is a key resource that defines plant growth in mature mangrove forests (McKee, 1995b; Chen and Twilley, 1998). A greater leaf area, for example, may benefit seedlings in a mangrove understory that are limited by light; understory light can be attenuated to 1.8–3.4% of ambient levels (Sherman et al., 2001). Under such conditions, enhanced leaf area index (area of leaves per unit area of land) would allow competitive growth responses to gaps of light in a forest that may form from small-scale disturbances that result in loss of tree canopy such as lightning, wind disturbance, or other mechanisms causing tree fall (light gaps). The relative competition of mangrove species in areas of light that are formed from these disturbances in dense forest provides insight into the relative tolerance to shaded conditions (shade tolerance). Three broad groups of mangroves related to light adaptation are (i) those which appear to be somewhat shade tolerant both as seedlings and as adults, (ii) those which appear to be shade intolerant, and (iii) those which shift light tolerance between seedling and tree stage, such as intolerant as seedlings and tolerant as trees and vice versa (Saenger, 2002). There is no clear pattern among mangrove genera and some species have evidence of both strategies in different environmental conditions (Krauss et al., 2008). In general, although, the growth of mangroves saturates at lower light levels than most other plants and is thus considered to be shade tolerant. However, in the neotropics, it is evident that *Laguncularia* is one of the more shade-intolerant species and has elevated growth capacity under high light conditions.

Recruitment of mangrove saplings, which depends on seedling vigor under a mangrove canopy, dominates community regeneration processes after a light gap is formed (Chen and Twilley, 1998). Models and theories of plant growth indicate that, in response to resource variation, plants partition photosynthates to optimize resource capture and consequently maximize growth rate (Shipley and Meziane, 2002). Implicit in these ideas is the prediction that plants will adjust their allocation in above- and belowground mass to compensate for that resource, which is in short supply (Tilman, 1988; Bazzaz, 1990; Chapin et al., 1990; Gleeson and Tilman, 1992). These plant strategies in biomass allocation are also found in mangroves, but the effects of salinity complicate the relative compensation of resource acquisition since salt uptake may regulate these processes. For example, the increased cost of carbon acquisition per unit of water and nutrient uptake in saline habitats (Ball, 1988a,b) suggests that mangroves exhibit an increased biomass allocation to shoots in low-light conditions and to roots with increasing salinity (Ball, 1988b). Most mangroves

are considered shade tolerant as described above, possibly because of this strategy to survive in salt water. Recent reviews highlight the interactive effects of light adaptation to salinity levels and conclude that many interactions with salinity may mask any specific definition as shade tolerance (Krauss et al., 2008). Those mangrove species that demonstrate higher allocation to aboveground resources under high light conditions, such as *Laguncularia*, are less competitive under higher soil salinity, but thrive when soils have low salinity and high nutrients (Krauss et al., 2008).

In the absence of regulators and light controlling plant growth, soil nutrient availability is often implicated as the principal factor determining variation in mangrove growth. Comparative analysis of mangrove forests and soil characteristics, in addition to fertilization studies, revealed that phosphorus (P) availability was one of the major factors limiting annual growth of mangrove forests (Feller, 1995; Feller et al., 1999, 2003; Twilley and Rivera-Monroy, 2009). A Monod model (Bridgham et al., 1995), which has the form shown in Figure 7.4 for resource gradients, describes how basal area (area of tree trunks per unit area of land) is strongly correlated with total soil P in new world mangroves at sites where soil salinity were all less than 50 psu (Twilley and Rivera-Monroy, 2009). The significant fit of soil P to a Monod model of tree basal area demonstrates that there is some upper limit of resource concentration that growth no longer increases (similar to concept of substrate saturation in enzyme kinetics). The half-saturation constant of soil P based on this Monod model was 0.12 mg/cm^3, which indicates that concentrations around this value will limit plant growth. This is consistent with studies of mangroves in carbonate-dominated environments in the greater Caribbean that show significant P-limitation of mangrove productivity under soil concentrations of about 0.06 mg/cm^3. When these soil P concentrations are elevated with fertilization, there is a significant response in prop root and stem elongation.

7.1.5 Complex Soil Interactions

Sulfate reduction forms hydrogen sulfide, which will react to form pyrite, elemental sulfur, or iron monosulfides (Holmer et al., 1994). These biochemical pathways that dominate formation of reduced zones can strongly influence phosphate availability along inundation gradients (or seasonally inundated soils). Under oxidized conditions in the presence of iron, phosphorus becomes adsorbed onto iron oxyhydroxides resulting in occluded forms of phosphorus and reducing the concentration of soluble reactive phosphorus in mangrove pore waters (Holmer et al., 1994; Sherman et al., 1998). Under anoxic conditions in the presence of sulfate and iron, sulfate reduction results in the formation of iron sulfides, mostly pyrites, and phosphorus goes back into solution in pore waters. This process of increasing phosphorus solubility, and thus resource availability in mangrove pore waters, may vary along the intertidal zone, depending on the supply of oxygen, supply of sulfate, and the availability of iron.

The spatial and seasonal inundation of mangrove soils establishes complex zones of oxidized and reduced sediments that control the distribution of regulators and resources. When oxygen is absent and both sulfate and iron are present, the pyrite-forming potential is high and thus increases phosphorus solubility potential (Sherman et al., 1998; Gleason et al., 2003). When pyrite is oxidized in the transition from reduced to oxidized zones in mangrove soils, sulfate and acidity are by-products as in the formation of iron oxyhydroxides that reduce the solubility and migration of phosphorus in the soil column (such as across the sediment–water interface). Iron can play a pivotal role in how such limitation in muddy environments is expressed in mangrove growth. In the presence of iron under anaerobic respiration, there are two important reactions that affect regulator and resource gradients in mangrove soils: (i) iron reacts with sulfide to reduce hydrogen sulfide toxicity and phosphorus is released into solution of mangrove pore waters; (ii) in the absence of iron, sulfate reduction forms hydrogen sulfide and phosphorus becomes bound to calcium carbonate minerals that remain insoluble under these conditions. Iron can be a key nutrient that will determine the level of regulators that control mangrove productivity. This interaction between resource (iron) and regulator (HS$^-$) is a function of hydroperiod along the intertidal gradient. This complex interaction of both regulators and resources confuses the specific nature of what limits plant growth in many environments. It is most likely that several mechanisms along an intertidal gradient and seasonally within a zone can contribute to limited growth conditions and thus lead to a stressed environment.

7.2 ECOSYSTEM STRUCTURE AND FUNCTION

7.2.1 Ecogeomorphology

The complex interaction of geophysical processes and ecological response to resources, regulators, and
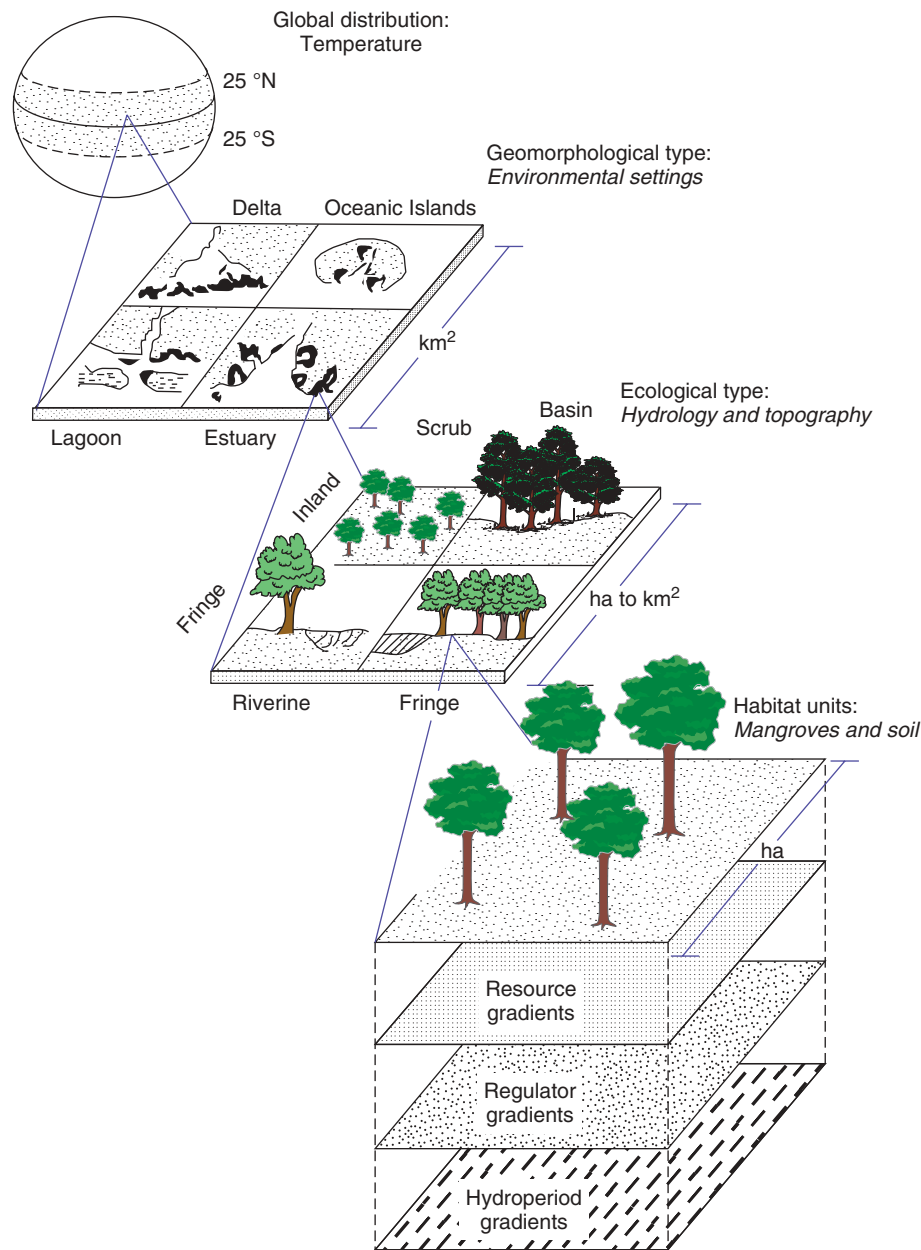
FIGURE 7.6 Hierarchical classification system to describe patterns of mangrove structure and function based on global, geomorphological (regional), and ecological (local) factors that control the concentration of nutrient resources and regulators in soil along gradients from fringe to more interior locations from shore. *Source:* Modified from Twilley et al. 1998 and Twilley and Rivera-Monroy (2005).

hydroperiod are captured in an ecogeomorphic classification of mangrove wetlands. This classification reflects a combination of spatial hierarchical levels that form patterns at different temporal scales that can explain global patterns across different coastal landforms (Fig. 7.6). The ecogeomorphic classification of mangrove wetlands describes the relative role of geophysical processes across different geomorphological settings (carbonate to muddy coasts)

and their interaction with ecological processes, which can account for much of the diversity in mangrove community structure and ecosystem function (Thom, 1982, 1984; Woodroffe, 1992; Twilley, 1995; Twilley et al., 1996; Woodroffe, 2002).

Climate and landform characteristics of a coastal region together with the relative influence of river, tides, and waves control the basic coastal settings of mangrove wetlands (Thom, 1984; Twilley, 1995;
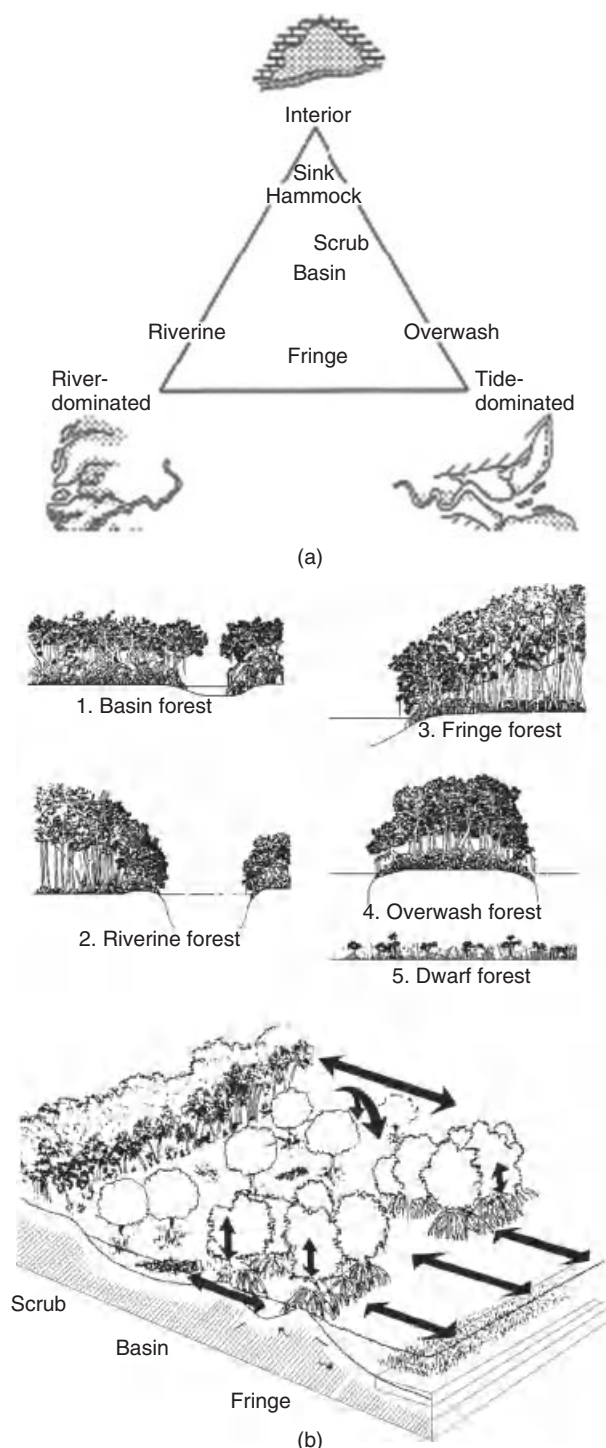
FIGURE 7.7 The geomorphological classification of mangroves by Woodroffe (2002) and ecological classification of Lugo and Snedaker (1974).

Woodroffe, 2002). At the global level, temperature distribution constrains the latitudinal expanse of mangroves along coastal landforms, and biogeographic provinces define which mangrove species will colonize the landscape (described above). Oceanic processes (tide and waves) and river input determine geomorphic settings by controlling the relative amounts of clastic and biogenic sediments (Woodroffe, 2002). River input of sediments is a function of catchment size, climate, and lithology. These factors along with geologic setting, topography, and hydrodynamic processes determine sedimentation that defines geomorphologic types. River-dominated coasts have the most extensive mangroves such as deltas associated with large tropical rivers. Deltas receive enormous sediment load from geologically young and tectonically active headwaters and are extremely dynamic. Tide-dominated coasts with high tidal range (>3 m) can have extensive low gradient intertidal zone available for mangrove colonization with gradients in hydroperiod and muddy to sandy conditions depending on local geology. Wave-dominated coasts usually have mangroves colonizing sandy ridges parallel to the shore that often function as barrier islands enclosing a series of elongate lagoons. Mangrove colonization may be more dominant along the back-barrier region of sediment infill and lower energy conditions. Along the carbonate shores of ocean islands, the topography of low versus high catchments inside the interior of the island defines environmental settings of mangroves. Low islands are dominated by carbonate sediment, whereas high islands under high rainfall conditions (Pacific Islands, >4 m annual precipitation) may have zones of alluvial sediment deposition. These geomorphologic types are not clearly delineated but represent a continuum in the relative effects of climate, river, waves, and tides on coastal processes that determine mangrove distribution.

These landform conditions establish the constraints of finer grain processes (referred to as *ecological processes*) that explain the variety of habitats within any one type of geomorphological setting (Fig. 7.7). In each of the coastal settings controlled by tides, waves, and rivers, local variations in topography and hydrology result in the development of distinct ecological types of mangrove wetlands such as riverine, fringe, and interior forests (Fig. 7.7; Lugo and Snedaker, 1974; Lugo, 1990; Woodroffe, 1992, 2002). Local-scale gradients in tidal and river processes form diverse mangrove types along the shoreline, and these processes change with increased distance perpendicular from the shore to more interior locations that can form

mangrove zones (Woodroffe, 2002). The lower intertidal zone consists of a streamside levee or berm that varies depending on the relative influence of river and tides. In river-dominated environments, the lower intertidal zone is classified as riverine, with monospecific zones of mangrove wetlands that are more robust in this lower intertidal zone (Lugo and Snedaker, 1974; Lugo, 1990). With more tidal influence and less river input of sediment, the lower intertidal zone is similar to the fringe mangrove zone that may consist of less muddy and sandier sediment. Intertidal environments dominated by tides are referred to as *overwash mangroves* of Lugo and Snedaker. All three of these ecological types may be considered fringe mangroves that occupy river-dominated (riverine) to tidal-dominated (overwash) environments (Fig. 7.7). The geophysical energy that impacts the development of mangrove soils can have strong influence on edaphic conditions such as fertility, redox conditions, metal concentrations, soil salinity, sandy versus muddy substrate, and hydroperiod, as described above.

The higher elevations of the upper intertidal zone are a different inundation class as defined above and can have different substrate and forest stature classified as interior forests (Fig. 7.7; Woodroffe, 2002). These interior forests include the basin, scrub, and hammock forests as per the classification by Lugo and Snedaker (1974). These interior forests are distinct from fringe forests as a consequence of reduced flood inundation patterns from rivers and tides as distance inland increases. Since river and tidal influence decreases within interior forests, the balance of water (hydroperiod) is controlled more by regional climate than by the geophysical properties of the coastal zone (Blasco, 1984). In drier climates with little upland freshwater input, more interior mangrove zones are less frequently inundated by tides resulting in more hypersaline soils with salinity ranging from 80 to 140 psu (Castaneda-Moya et al., 2006). In such dry climates, increased elevation results in more monospecific mangrove forests dominated by more salt-tolerant species, such as *Avicennia*. Salt stress will increase with distance from shore, and this distance can be correlated with shorter tree heights, forming scrub mangrove forests at the most interior locations (<3 m tall; Fig. 7.7). In perhumid coastal settings where evaporation potential exceeds precipitation, soil salinities of zones interior of mangrove wetlands are greater than 120 psu leading to formation of salt pannes or salinas that prevent colonization by all but the most salt-adapted plants (but no mangroves; e.g., Cintrón et al., 1978; Castañeda-Moya et al., 2006).

In moist climates, the interior zone may or may not be represented by mangrove vegetation with reduced stature, depending on the resource limitations in this zone with upland vegetation. In moist zones with significant upland runoff, the interior mangrove zone lack salinas and mangrove vegetation gradually mixes with freshwater vegetation, either marsh or forested wetlands, forming a continuous ecotone of vegetation with upland environments. There may be cases where scrub mangrove wetlands occur in the upper intertidal zone of moist landscapes, especially those on carbonate formations, where resources (nutrients, particularly P) may limit plant growth rather than regulators (hypersalinity). In the case of the Everglades, low nutrient resources are argued to be the key limiting factor to plant stature (Ewe et al., 2006). Mangrove scrub communities on the interior of carbonate islands along the coast of Belize have also been shown to be limited in stature by levels of phosphorus concentrations in soils (Feller, 1995).

In perhumid tropical regions where precipitation deficits occur, limits to mangrove zonation and forest structure can be modified by the presence of freshwater inputs to the coast from upland watersheds. Thus the amount of moisture in mangrove soils is a complex interaction of regional climate and hydrology, including upland freshwater input. Even though mangrove wetlands may be located in a dry climatic zone, they may have characteristic zonation of mangrove wetlands in humid coastal environmental settings because of the presence of freshwater inputs. Freshwater subsidies from upland watersheds increase the moisture of mangrove soils and influence the functional ecology of mangrove wetlands. The environmental subsidy of upland runoff will be an important consideration in the management of mangrove resources, as described in a later section of this chapter.

7.3 ECOLOGICAL PROCESSES

7.3.1 Zonation and Succession

Zonation in mangrove communities (Fig. 7.7) has variously been accounted for by a number of ecological factors including salinity tolerance of individual species (Snedaker, 1982), seedling dispersal patterns resulting from different sizes of mangrove propagules (Rabinowitz, 1978; Sousa et al., 2003), differential consumption by grapsid crabs and other predators (Smith, 1987; McKee, 1993; Sousa et al., 2003), seedling and sapling establishment (Ellison and Farnsworth,

1993; McKee, 1995a), and interspecific competition (Ball, 1980; Clarke, 2004). Disturbance regimes can also control structural attributes in mangrove forests especially simultaneous death of adult trees from lightning strikes (Smith et al., 1994). Among these factors, the establishment of seedlings and saplings is one of the most important processes in forest regeneration (Grubb, 1977; Harper, 1977). The establishment of new mangrove individuals is controlled not only by ecological processes such as herbivory (Onuf et al., 1977; Robertson et al., 1990) but also by the response of mangrove wetlands to physiological stress caused by resource shortages and regulator excess (Huston and Smith, 1987) in intertidal habitats that has been described in sections above (Ball, 1988a, 1996). And these processes will vary in fringe versus interior forests, as the combined effects of geophysical and ecological processes across diverse coastal landscapes form spatial and temporal patterns in forest structure along different inundation classes of the intertidal zone.

Many of the descriptions of plant zonation are based on mangrove physiognomy in relatively species-poor environments of the Caribbean Sea on carbonate platforms. Yet even in biogeographic regions of higher species diversity and muddy coasts, there are clear patterns in mixed species associations and tree physiognomy that define mangrove zonation (Watson, 1928). In other areas of the old world tropics, mangrove ecologists have not been able to define specific zonation patterns (Ellison, 2002). Global patterns are very hard to discern that are consistent across biogeographic or geomorphic regions, depending on the response of mangrove trees to the edaphic, geophysical, and climate conditions that constrain ecological processes described above. It is this hierarchy of physical and ecological constraints that define zonation in mangrove-dominated estuaries.

Succession in mangrove wetlands has often been equated with zonation (Davis, 1940), wherein ''pioneer species'' would be found in the fringe zones, and zones of vegetation more landward would ''recapitulate'' the successional sequence toward terrestrial communities. Yet as described above, ideas of succession based on species-poor regions of neotropics where zonation is more evident are not as clearly defined in more species-rich biogeographic regions where multiple patterns of forest distribution may occur. The establishment of stable monospecific zones was proposed wherein each species is best adapted to flourish because of the interaction of physiological tolerances of species with environmental conditions (Snedaker, 1982). Zones of mixed species composition

have been thought of primarily as transition zones or ecotones between monospecific zones, and as such have been interpreted as being temporary responses to disturbance (Lugo and Snedaker, 1974; Lugo, 1980). However, analysis of long-term vegetation transects (Ellison, 2002) and geological surveys of intertidal zone (Thom, 1967) have shown that mixed associations of mangroves may be stable communities of stable coastal landscape. The zonation and structure of mangrove wetlands are responsive to eustatic changes in sea level and that mangrove zones can be viewed as steady-state zones migrating toward or away from the sea, depending on rate of change in both sea levels and land surface. In areas of subsidence or unstable landforms, there may be different patterns of vegetation response to relative rise in water levels. In most coastal landscapes, both monospecific and mixed vegetation zones of mangrove wetlands represent steady-state adjustments rather than successional stages (Lugo, 1980; Snedaker, 1982).

The trajectory of vegetation dynamics are constrained by the geomorphological and climatic characteristics of coastal environments, and modified by the ecological interactions within a mangrove forest. Thus, general patterns may be observed within geographic regions, but there are diverse patterns globally based on different landforms that occur in tropical biogeographic regions. In addition, changes in environmental settings caused by drought, subsidence, or tropical cyclones can interrupt patterns in vegetation development (Roth 1992). Since seldom do we have sufficient long-term records to distinguish these patterns in mangrove wetlands, there are no models of mangrove succession that can be applied outside specific geographical boundaries (Berger et al., 2008). A simulation model of mangroves in the Shark River estuary of south Florida (Chen and Twilley, 1998) showed that at least 200 years of forest development without disturbance was necessary to express the steady-state dominance of mangrove species, although the maximum basal area and biomass may be obtained in nearly 30 years following hurricane disturbance. It is therefore rare in many coastal regions to find ''old growth'' mangrove forest that are not remnants of recent disturbances. Although hurricanes may stimulate certain ecological processes in coastal ecosystems (Conner et al., 1989), forested wetlands such as mangroves in many tropical coastal regions are susceptible to damage from high winds and hurricanes (Zhang et al., 2008; Smith et al., 2009), and the normal frequencies of this region can result in a dominance of young successional forests (Lugo, 1980).

7.3.2 Biomass and Productivity

Tree height and aboveground biomass of mangrove wetlands throughout the tropics decrease at higher latitudes (Fig. 7.8a), indicating the constraint of climate on forest development in warm temperate regions (Twilley et al., 1992; Saenger and Snedaker, 1993). Aboveground biomass in the lower latitudes is about 300 Mg/ha (with standard error of about 75 Mg/ha) compared to about 100 Mg/ha at the higher latitudes. It is interesting that mangrove biomass at 20°—30° north and south latitude are about half of the values near the Equator (Twilley et al., 1992). Values are not shown, but about 40% of the aboveground biomass is found belowground, which is higher than in most other wetland forests (from Saenger, 2002). Most biomass estimates are based on some allometric relation with tree diameter and height (Brown and Lugo, 1982). There have been excellent summaries of these equations for specific species (Saenger, 2002), with one that is considered of value for all mangrove wetlands to estimate aboveground biomass: $AGB = 116.6[(DBH)^2 H]^{0.8877}$ (from Komiyama et al., 1988). There is an agreement for generalized curves of *Rhizophora* against DBH based on data for *Rhizophora apiculata, Rhizophora mucronata, R. mangle*, and *Rhizophora racemosa* (Saenger, 2002). Also, there is a relation for *Rhizophora stylosa* that belowground biomass is equivalent to aboveground biomass multiplied by 0.394 (Komiyama et al., 1987).

Mangrove biomass can vary dramatically within any given latitude (note standard errors on Fig. 7.8a), an indication that local effects of resources, regulators, and hydroperiod (discussed above) may significantly limit the potential for forest development at all latitudes. The interactions of these three gradients have been proposed as a constraint envelope for defining the productivity of mangrove wetlands based on the relative degree of stress conditions (Fig. 7.4; Twilley and Rivera-Monroy, 2005). At low levels of stress for all three environmental gradients, mangrove wetlands will reach their maximum levels of biomass and net ecosystem productivity, such as along muddy coasts in low-latitude regions with low frequency of disturbance. Extensive mangrove areas of high productivity occur along the Niger delta, Bangladesh, Fly River delta, Usamacinta delta, and French Guinea. Coastal settings that result in higher stress conditions for any one or more of these gradients have lower total net primary productivity. In the description of zonation above, fringe environments of river-dominated coastal settings have the most fertile and least stressed environments resulting in highest levels of net primary productivity. More stress conditions develop
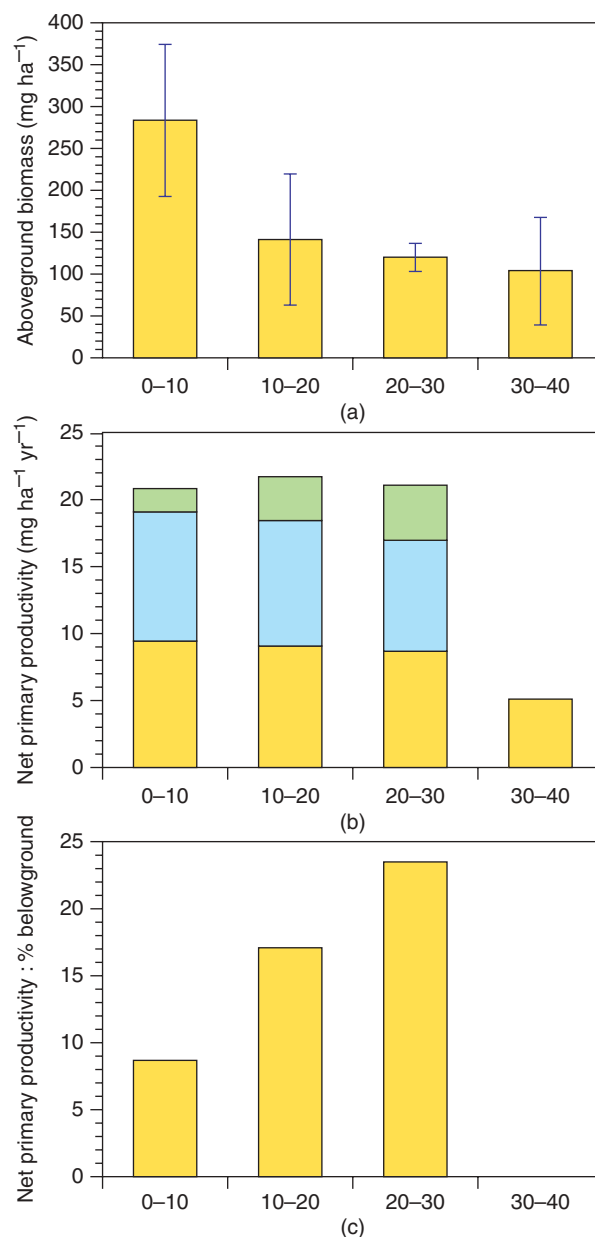
FIGURE 7.8 Mangrove biomass and net primary productivity grouped by latitude including (a) aboveground biomass, (b) net primary productivity, and (c) net production/biomass ratios. In panel (b), yellow is litterfall, blue is wood production, and green is fine root production.

by moving toward more tidally dominated coastal settings, and interior where there is less inundation (thus more control by dry vs humid climates). As described above, dry interior climates result in elevated soil salinities and can be a major determinant of net primary productivity in many coastal environments (Fig. 7.8b).

There are now extensive surveys of mangrove net primary productivity that include litter fall,

wood growth, and root production (mainly fine roots). When these results are compared across latitude, they demonstrate a very interesting pattern of consistent total net productivity of about 21 Mg/ha/year (Fig. 7.8b). This means that the production/biomass ratio for mangroves varies considerably with latitude, approximately 0.08 at low latitudes and 0.20 in the upper region of the tropics. Litter fall across this latitude gradient is about 10 Mg/ha/year and wood production is nearly equivalent at about 9 Mg/ha/year. Fine root production is much less at about 2–5 Mg/ha/year, with rates increasing at higher latitudes. In fact, the percent of total net productivity that occurs belowground increases from about 9% in the low latitudes to about 25% at latitudes between $20°$ and $30°$ north or south (Fig. 7.8c). There are fewer estimates of fine root production than litter fall or wood, and this component of root production may be lower than total root production estimates (Cormier, 2003). But it is evident that litter fall is only half of the total net primary productivity of mangrove wetlands and that for most of the tropics these are very productive forests in the coastal landscape.

Litter fall from a mangrove canopy is dominated by leaf fall with the remainder fraction consisting of wood (stems from the canopy), grass, and reproductive parts (Fig. 7.9a). Leaf fall is continuous year round but with seasonal rates that in the Caribbean is during fall months of September to November. Seasonal and temporal rates for five years at the FCE LTER are consistent, with the reproductive input from the canopy highest in late summer, just before peak leaf fall from the canopy. A mean leaf fall rate for mangrove wetlands in the Caribbean region is about 2 g dry mass m^2/ day or about 750 g/m^2/year. Regional rates in litter production in mangrove wetlands are generally a function of the production envelope described above, and rank among the ecological types as follows: riverine > fringe > interior > scrub (Pool et al., 1975; Twilley et al., 1986; Ewe et al., 2006; Fig. 7.9b). The fate of leaf litter on the forest floor in most upland forests is controlled by rates of decomposition, thus the residence time of litter will vary with local environment together with chemical characteristics of leaf tissue, and most temperate forests have leaf litter residence time of about 1 year. Mangrove leaf litter decomposes much faster than most upland temperate forests and even tropical moist forests, with average residence time about 0.6 year. *Rhizophora* has slower decomposition rate than *Avicennia* and *Sonneratia* with corresponding residence time of 2–3 months.

A unique feature of mangrove forests compared to upland or other forested wetlands is the daily influence of tides on leaf litter export to adjacent coastal waters. Leaf litter represents a potential source of organic matter and nutrients that may be transported to adjacent coastal waters, facilitated by some species because of the buoyant nature of senescent leaves (Fig. 7.10). The export of this leaf litter by the bidirectional flow of tides can transport organic matter that supports commercially important fisheries (Odum and Heald, 1972; Macnae, 1974; Thayer et al., 1987; Yáñez-Arancibia et al., 1988; Robertson and Duke, 1990). The dynamics of mangrove leaf litter, including productivity, decomposition, and export, can determine the coupling of mangrove wetlands to the secondary productivity and biogeochemistry of coastal ecosystems (Twilley, 1988; Alongi et al., 1992; Robertson et al., 1992; Twilley et al., 1997). Patterns of leaf litter turnover may be specific among the ecogeomorphological types of mangrove wetlands depending on the ecological type and the environmental setting (Lugo and Snedaker, 1974; Twilley et al., 1986, 1997). Accordingly, the rank of leaf litter turnover is usually riverine > fringe > basin with greater litter export in sites with increasing tidal inundation (Fig. 7.9b).

Several studies in the old world tropics in higher energy coastal environments of Australia and Malaysia have emphasized the influence of crabs on the fate of mangrove leaf litter (Malley, 1978; Leh and Sasekumar, 1985; Robertson, 1986; Robertson and Daniel, 1989; Lee, 1989; Camilleri, 1992; Imgraben and Dittmann, 2008). In these coastal environments, a strictly geophysical model of litter dynamics is limited for many mangrove sites where crabs consume 28–79% of the annual leaf fall (Robertson, 1986, 1988; Robertson and Daniel, 1989). These studies suggest that biological factors may influence leaf litter turnover more than the geophysical processes as suggested in Twilley et al. (1986) for new world mangrove wetlands. A study in the Guayas River estuary in Ecuador found that the fate of leaf litter in new world mangrove wetlands was influenced by the crab *Ucides occidentalis*, similar to the studies of crab processing of leaf litter in the old world tropics (Twilley et al., 1997). Rates of litter turnover in mangrove wetlands with crabs in both hemispheres are similar, and much higher than in wetlands with minor influence of crab consumption on leaf litter dynamics. Differences in litter turnover rates among mangrove wetlands are a combination of species-specific degradation rates, hydrology (tidal frequency), soil fertility, and biological factors such as crabs, which influence the rates of litter dynamics.
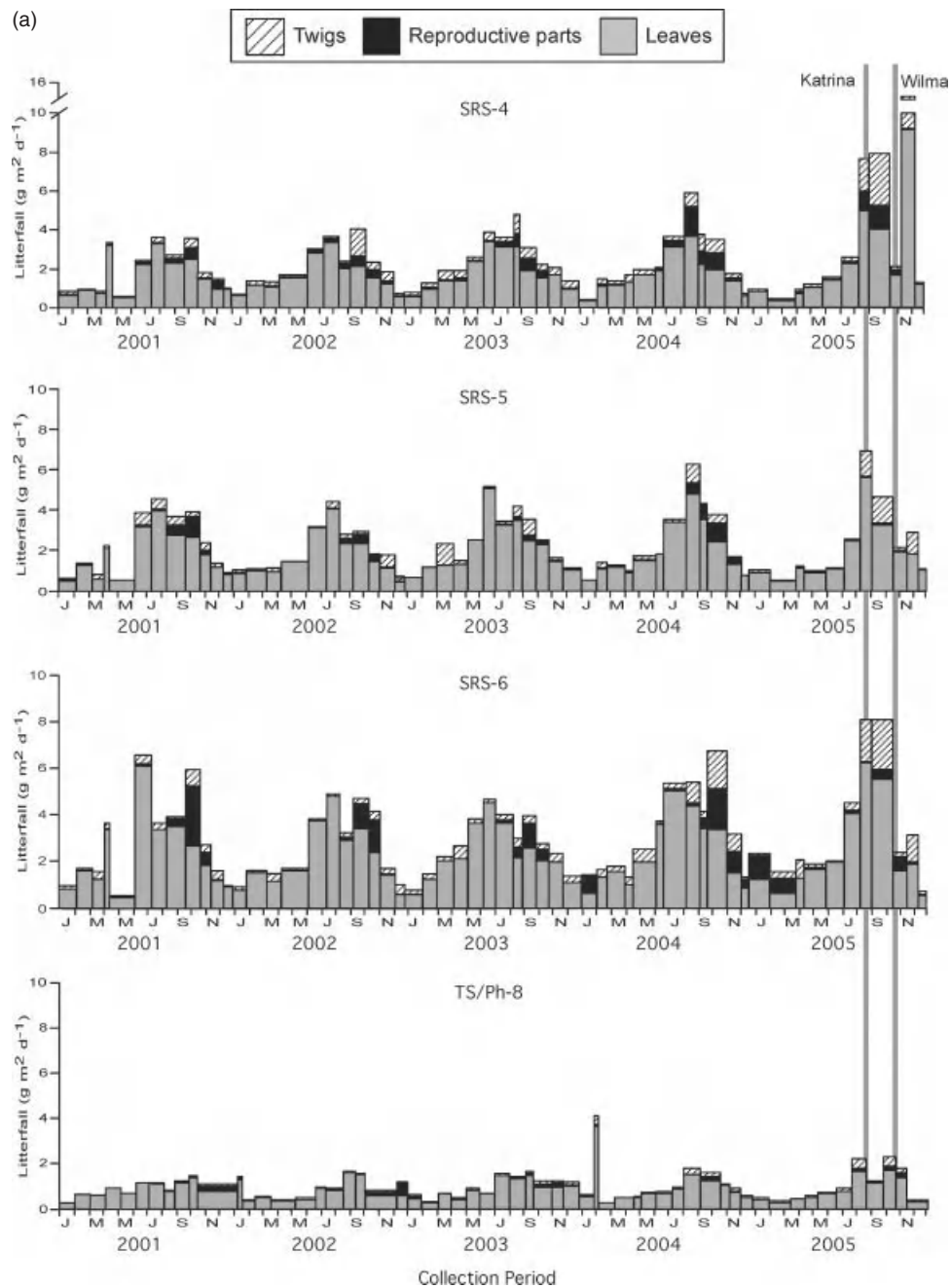
FIGURE 7.9 (a) Litter fall for 5 years at four sites in the Florida Coastal Everglades (from Castañeda 2010). (b) Summary of organic matter input (litter fall) and loss (export and decomposition) for different ecological type of mangrove based on studies in neotropics. (After Twilley et al. 1986 as modified by Mitsch and Gosselink 2000).

Mangrove crabs are less abundant in mangrove wetlands of the Gulf of Mexico and Caribbean (Jones, 1984), suggesting that they have less influence on ecological processes in mangrove wetlands of this region. However, where they do occur in significant numbers, mangrove crabs can have a significant influence on litter dynamics.

Carbon export from mangrove ecosystems ranges from 1.86 to 401 gC/m^2/year (Twilley et al., 1992), with an average rate of about 210 gC/m/year (Table 7.2; Twilley and Rivera-Monroy, 2009). Carbon export from mangrove wetlands is nearly double the rate of average carbon export from salt marshes (Nixon, 1980), which may be associated with the more
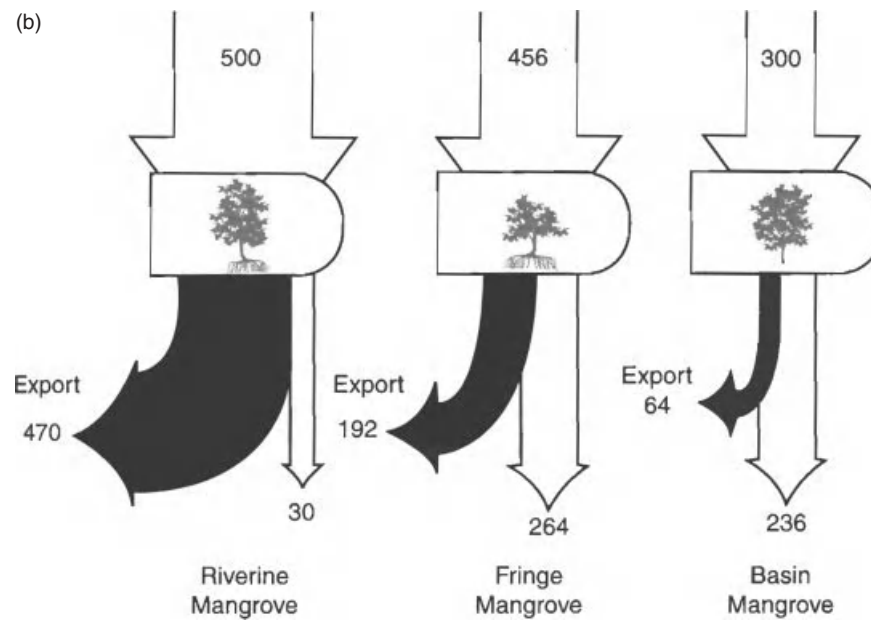
FIGURE 7.9 (*Continued*)

TABLE 7.2 Summary of literature data on particulate, dissolved, and total organic carbon (POC, DOC, and TOC) export from mangroves

Site/Country	POC Export	DOC Export	TOC Export	Data Source
Florida (United States)	—	—	186	Heald (1969)
Florida (United States)	—	—	292	Odum and Heald (1972)
Florida (United States)	—	—	91	Lugo and Snedaker (1974)
Australia	420	—	—	Boto and Bunt (1981)
Florida (United States)	16	48	64	Twilley (1985)
Malaysia	—	—	176	Gong and Ong (1990)
New Zealand	110	—	—	Woodroffe (1985)
Australia	—	—	332	Woodroffe et al. (1988)
Australia	340	—	—	Robertson (1986)
Australia	—	—	−7	Boto and Wellington (1988)
Hong Kong	2	—	—	Lee (1989)
Hong Kong	5	—	—	Lee (1990)
Australia	—	—	994	Alongi et al. (1998)
Papua New Guinea	—	—	343	Robertson and Alongi (1995)
Zanzibar (Tanzania)	65	230	295	Machiwa (1999)
Brazil	—	44	—	Dittmar and Lara (2001a)
Florida (United States)	—	56	—	Romigh et al. (2006)
Brazil	—	144	—	Dittmar et al. (2006)
Florida (United States)	—		7.1	Sutula et al. (2003)
Florida (United States)	—	381	—	Davis et al. (2001)

Fluxes are expressed in grams of carbon per square meter per year.
Source: Adapted from Twilley et al. (1992), Lee (1995), and recently published by Bouillon et al. (2007).

buoyant mangrove leaf litter, higher precipitation in tropical wetlands, and greater tidal amplitude in mangrove systems studied (Twilley, 1988). The fate of mangrove primary production has been a major topic of debate in the literature during the past decades (Bouillon et al., 2008a). In particular, the

''outwelling'' hypothesis, first proposed by Odum and Heald (1975), suggested that a large fraction of the organic matter produced by mangrove trees is exported to the coastal ocean, where it would form the basis of a detritus food chain and thereby support coastal fisheries (Fig. 7.10). Despite the large number

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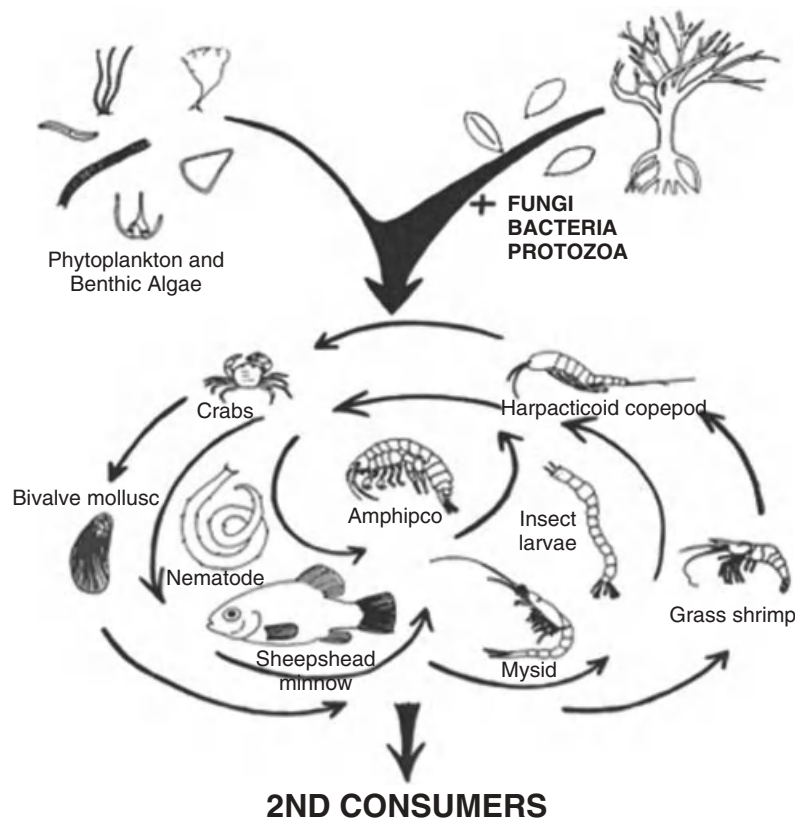
FIGURE 7.10   Schematic of the detrital food chain of the North River estuary in Everglades National Park. From Odum and Heald 1972.

of case studies dealing with various aspects of organic matter cycling in mangrove systems (Kristensen et al., 2008), there is still no consensus on overall mangrove primary production and the ecological fate of the organic matter produced (Bouillon et al., 2008b).

Several authors have suggested that mangrove-derived organic matter is of global significance in the coastal zone (Robertson and Alongi, 1995; Schlunz and Schneider, 2000; Dittmar and Lara, 2001b). Estimates indicate that mangrove forests could be responsible for ~10% of the global export of terrestrial particulate organic carbon (POC) and dissolved organic carbon (DOC) to the coastal zone (Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006, respectively) and for ~10% of the global organic carbon burial along with sea grasses in the coastal ocean (Duarte et al., 2005). The exchange of carbon between tidal wetlands such as mangrove forests or salt marshes and the coastal ocean, and its ultimate fate in the ocean is therefore increasingly recognized as a potentially important component in the ocean carbon budget (Twilley et al., 1992). This may particularly be evident in river-dominated mangrove systems such as muddy coasts and deltas, where organic material

exchanged is greater at the boundary of the forests compared to other coastal settings (Twilley, 1985).

7.3.3 Nutrient Biogeochemistry of Mangrove Wetlands

The biogeochemistry of mangrove wetlands includes the fate and effects of sediment, nutrients, organic matter, dissolved gases, trace elements, and toxic substances on ecological properties as a function of diverse coastal landscapes (Fig. 7.11). The function of mangrove wetlands as either a nutrient source or a sink depends on the process of material exchange at the interface between mangrove wetlands and the estuary, which is largely controlled by tides as described above. The specific nature of material flux at the estuarine interface is controlled by the balance of many ecological processes within the mangrove wetland, and therefore, exchange is not strictly dependent on the geophysical properties of an estuary. Defining the relative influence of ecological and geophysical processes associated with the biogeochemical functions of mangrove wetlands as sink, source, or transformer of nutrients is clearly one of the most complex properties of these ecosystems.
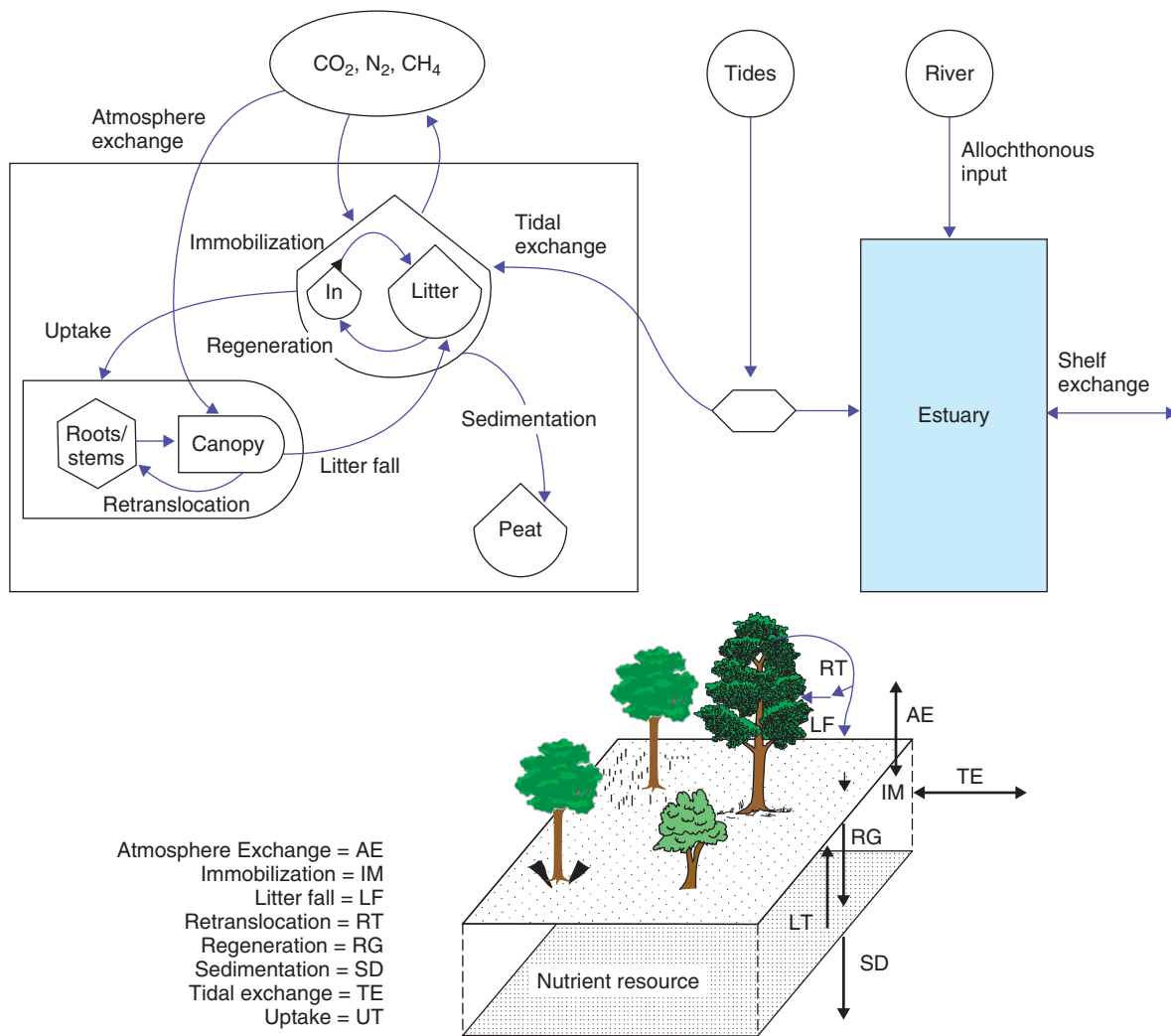
FIGURE 7.11 Biogeochemistry pathways in mangrove forests. *Source:* Modified from Twilley and Rivera-Monroy 2009.

Nutrient exchanges may occur with either coastal waters (TE) or with the atmosphere (AE), depending on whether the nutrient has a gas phase (Fig. 7.11). For instance, P dynamics in mangrove wetlands is representative of a sedimentary cycle and is restricted to allochthonous input from the river or coastal environments and redistribution by tides or storm events. However, substantial amounts of carbon and nitrogen can exchange with the atmosphere depending on the balance of certain biochemical processes. Thus the nitrogen cycle of mangrove wetlands is very complex with several mechanisms both at the interface with coastal waters and with the atmosphere that influence the mass balance of this nutrient. In addition, there are processes of nutrient uptake, recycling, and remineralization that cycle nutrients among the canopy and soils of mangrove wetlands. These nutrient cycles are

similar to those described for other forested wetlands including root uptake (UT), retranslocation in the canopy (RT), litter fall (LF), decomposition (RG), immobilization (IM), and sedimentation (SD) (Fig. 7.11). One of the global hypotheses in mangrove nutrient biogeochemistry, as with other wetlands, is that the balance of these nutrient flows will determine the exchanges across the wetland boundary.

Evidence of nutrient resource limitation in mangroves can be evaluated by summarizing existing information on soil nutrient density among mangrove forests (68 measurements summarized in Fig. 7.12a). Nearly one third of the sites have total P density $< 0.10\,\text{mg/cm}^3$ representing mangroves in either interior carbonate settings (isolated from hurricane deposits), or interior lagoon settings with limited sediment input (such as basin sites at Rookery Bay
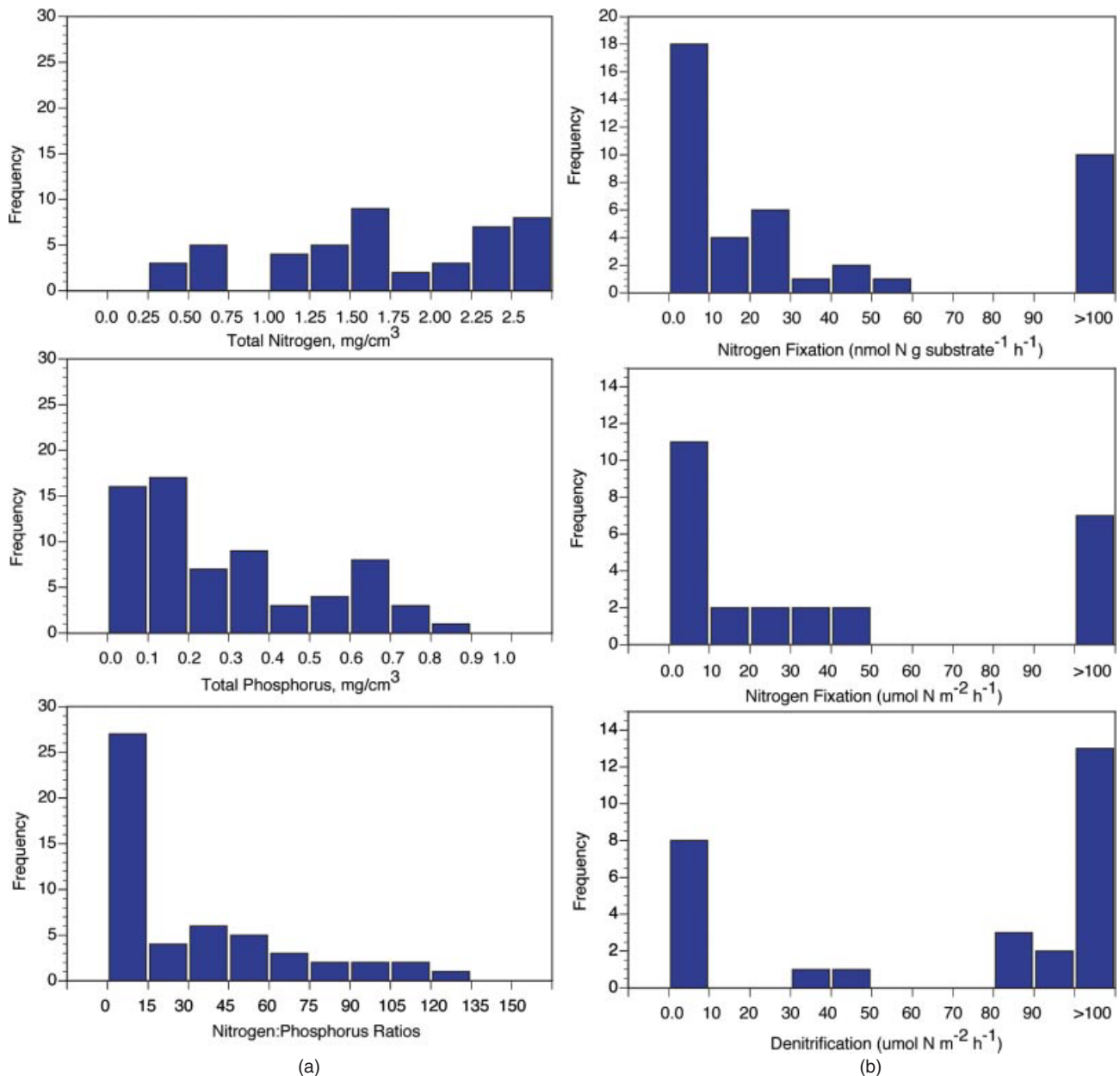
FIGURE 7.12 Survey of nutrient density (upper panel is total nitrogen and middle panel is total phosphorus) from sixty-eight mangrove sites around the world (based on mg per volume of sediment). Lower panel is the nitrogen/phosphorus ratio (atomic) of these nutrient concentrations for each respective site. (b) Survey of nitrogen fixation rates and denitrification rates based on literature values reported in Twilley and Rivera-Monroy (2009).

and Terminos Lagoon). Nearly half of these mangrove sites surveyed have N:P ratios >15, indicating that P is potentially limiting under those conditions (see discussion above on half saturation constant for mangrove biomass). However, both of these surveys demonstrate that nitrogen is potentially limiting in many locations where sediment deposition in estuarine and muddy coasts provide P density in soils sufficient to saturate growth conditions. This trend in

the relative content of N and P among mangrove sites in muddy, estuarine and carbonate settings is probably one of the strongest linkages between geomorphological settings and ecology of mangrove wetlands (Thom 1967).

The net exchange of nitrogen gas in mangrove ecosystems depends on the inputs of nitrogen via fixation relative to the loss via denitrification (Fig. 7.12b). The fixation of nitrogen depends on organisms that

utilize the nitrogenase enzyme in specific environments. The flux of nitrogen gas out of mangrove ecosystems is associated with nitrate reduction as part of organic respiration in the reduction zone known as *denitrification*. Thus the distribution of oxidized and reduced zones in mangrove soils in response to water levels (hydroperiod), together with the supply of oxidized form of nitrogen as NO_3, will determine the net balance of this nutrient in mangrove forests (Rivera-Monroy et al. 1996).

Nitrogen fixation represents the ''new'' source of nitrogen to the system and is the only process that can compensate for nitrogen removal by denitrification (Howarth et al., 1988). Nitrogenase activity has been observed in decomposing leaves, root surfaces (prop roots and pneumatophores), and sediment, but few of these studies have interpreted these rates relative to the nitrogen budget of mangrove forests (Twilley and Rivera-Monroy, 2009). These studies have shown that decaying mangrove leaves are sites of particularly high rates of fixation and thus may account for 15–64% of nitrogen immobilization during decomposition of mangrove leaf litter on the forest floor (Gotto et al., 1981; van der Valk and Attiwill, 1984; Woitchik et al., 1997). Sediment and roots fix nitrogen in range from nondetectable to about 15 nmol N/g of substrate/h, rates for leaf litter are commonly greater than 250 nmol N/g of substrate/h (Fig. 7.12a). Pelegri et al. (1997) estimated that N fixation could account for 45–100% of the total nitrogen immobilized in leaf litter (1–8 mg N dry/wt nitrogen enrichment) in the Shark River mangrove sites of the Florida Coastal Everglades. However, nitrogen fixation only could supply 7% (8.3 mg N/m^2/ day) of the N required (53 mg N/m^2/ day) for mangrove growth into this forest. Most of the studies of N fixation in mangrove wetlands average around 50 μmol/m^2/h, which is about 0.4% of the NPP of mangrove wetlands (Bouillon et al., 2008a).

Denitrification is primarily dependent on the presence of a reduction zone, an energy source, and availability of NO_3^- source. On the basis of the sources of NO_3^-, there are two types of denitrification: direct denitrification that is fueled by NO_3^- diffusing from the overlying water column into sediments, and coupled nitrification–denitrification that is supported by NO_3^- from nitrification in the sediments (Nielsen, 1992). The contributions of these two NO_3^- sources are regulated by different mechanisms. Direct denitrification is typically a linear function of the NO_3^- concentration in the overlying water and an inverse linear function of the oxygen penetration depth in the sediments (Christensen et al., 1990; Nielsen et al., 1990). Coupled nitrification–denitrification is regulated by the rate and position of nitrification activity, which in turn, is regulated by the nitrification capacity and the availability of ammonium and oxygen and is generally enhanced by deeper oxygen penetration (Henriksen and Kemp, 1988; Blackburn et al., 1994).

Mangrove sediments have a high potential for the removal of N from surface waters with a large range in denitrification estimates (Twilley and Rivera-Monroy, 2009). When reviewing the rates of nitrogen fixation and denitrification both on per mass and per area basis, it is clear that extreme values dominate the description in mangrove wetlands (Fig. 7.12b). There are rates either less than 10 μmol/m^2/h or greater than 100 μmol/m^2/h, at nearly equal frequency, for both fixation and denitrification. There is a slight evidence that denitrification may dominate the net flux based on this survey, but few comprehensive studies have evaluated both processes to the net nitrogen balance of mangrove ecosystems. And there is no evidence that either process may dominate mangrove wetlands in specific coastal setting or ecological type. A general average rate of denitrification among mangrove sediments is about 180 μmol/m^2/h, about four times that of nitrogen fixation. This is similar to the medium range of rates measured in mangrove sediments described by Nedwell (1975).

Sponges, tunicates, and a variety of other forms of epibionts on prop roots of mangrove wetlands are highly diverse (Sutherland, 1980; Rützler and Feller, 1988; Ellison and Farnsworth, 1992), especially along carbonate shorelines with little terrigenous input. The diversity and biomass of these communities and associated ecological functions may be limited to specific geomorphologic types that are protected from turbid waters. There are a few studies on ecosystem function that indicate that these communities are sites of nitrogen fixation that influence the nitrogen budget of mangrove canopies. There is evidence that epibionts on prop roots may be a source of nutrition for higher level predators as well as influencing various processes in mangrove fringe forests. These processes of nutrient regeneration associated with sponge communities that colonize aerial root systems of mangrove wetlands have received comparatively little attention, but they may influence the productivity of fringe mangrove forests, as well as enhance the exchange of nutrients with coastal waters (Ellison et al., 1996). The specific contribution of these productive and diverse epibiont communities in predominately carbonate environments may demonstrate an important linkage between biodiversity and ecosystem function.

TABLE 7.3 The annual accumulation of inorganic sediment (IS), organic sediment (OS), total carbon, total nitrogen, and total phosphorus in a variety of mangrove sites

Site Description			Inorganic Sediment (IS) (g m^{-2} yr^{-1})	Organic Sediment (OS) (g m^{-2} yr^{-1})	Total Carbon (g m^{-2} yr^{-1})	Total Nitrogen (g m^{-2} yr^{-1})	Total Phosphorus (g m^{-2} yr^{-1})	IS:OM	Reference
Country or Region	Estuary	Mangrove Type							
Southwest Florida	Rookery Bay	Interior	239.1	246.8	114.5	6.64	0.23	0.97	Lynch et al. 1989
		Interior	184.5	227.4	106.5	6.32	0.25	0.81	
		Interior	141.5	280.1	132.9	7.22	0.24	0.51	
		Interior	172.2	272.0	126.1	7.60	0.21	0.63	
		Fringe	307.8	54.7	32.2	1.34	0.27	5.62	
		Fringe	173.1	100.2	51.5	1.97	0.62	1.73	
Belize	West Pond	Fringe	93.64	276.1	122.4	5.77	0.16	0.34	Lynch et al. 1989
	Sittee River	Riverine	1286.4	307.9	129.6	7.95	1.06	4.18	
Terminos	Estero Pargo	Fringe	744.8	348.9	157.0	11.01	0.63	2.13	Lynch et al. 1989
Lagoon		Interior	386.7	231.6	104.2	4.83	0.21	1.67	
	Boca Chica	Riverine	1440.9	400.7	189.8	8.44	0.82	3.60	
		Riverine	1136.5	145.5	65.4	2.46	0.73	7.81	
Ecuador	Guayas River	Riverine	3581.6	803.3	287.8	10.07	3.01	4.46	Twilley et al. 2000
		Riverine	4318.8	813.9	265.5	10.41	3.62	5.31	
	Guayas River	Riverine	3076.4	997.4	387.5	13.37	0.92	3.08	
Gulf of Thailand	Sawi Bay	Riverine	7500		225.6	8.18			Alongi et al. 2001, 2004
Matang Forest		Riverine	2450		127	13.29			Alongi et al. 2004
		Riverine	3800		109.5	14.31			
		Riverine			100.7	17.89			

Sediments suspended in the water column are deposited in mangrove wetlands during flooding, and this allochthonous material enriches mangrove soils. Mangrove wetlands are considered land builders because of the high sediment-binding capacity of the root system (Scoffin, 1970). Comparing sedimentation rates across sites in new world tropics using techniques developed by Lynch et al. (1989), accumulation of organic matter among all sites while accumulation of inorganic matter was higher in the forests influenced by river discharge. The contribution of inorganic material ranges from 133 to 5151 g/m^2/year with higher values (>4000 g/m^2/year) occurring in riverine mangrove forests such as the Guayas River estuary, which represents a riverine type of coastal setting (Table 7.3; Twilley and Rivera-Monroy, 2009). Those sites with

sedimentation rates less than 500 g/m^2/year include the fringe and basin sites of Rookery Bay, and the lowest rate of 94 g/m^2/year of sediment input is to a fringe carbonate site in Belize. The IS/OM ratio of inorganic (IS) and organic (OM) sedimentation explains the effects of geophysical processes on sedimentation patterns in mangrove wetlands. The ratios are less than 1 in the basin sites at Rookery Bay and the carbonate site in Belize. The overwash site at Rookery Bay and fringe and basin site in Terminos Lagoon have ratios that range from 1.7 to 2.1, while the subtidal fringe site has a ratio of 5.6. All the riverine sites have ratios that range from 3.6 to 7.8 (Table 7.3).

Total nitrogen accumulation ranged from 1.34 g/m^2/year in the subtidal fringe in Rookery Bay to 11.01 g/m^2/year in the fringe forest at Terminos Lagoon (Table 7.3). There is no clear

pattern among ecological types or geographical locations. The accumulation of nitrogen among the riverine and basin forests was similar at about 5.5 g/m^2/year, which is higher than the range of denitrification and nitrogen fixation described above. Thus nitrogen storage in sediment soils is an important fate of nitrogen in mangrove ecosystems. The accumulation of carbon (59–185 g/m^2/year) and nitrogen (1.55–5.80 g/m^2/year) was associated with deposition of organic matter and rates were similar among sites. Atomic carbon/nitrogen ratios of accumulated material at the riverine sites were greater than 30, whereas sites with less riverine input had C/N ratios less than 20. Accumulation of phosphorus ranged from 0.11 to 0.78 g/m^2/year and the higher rates occurred at sites with high inorganic matter loading. The elevated phosphate input rates into riverine mangrove sites are associated with higher levels of litter productivity compared to tidal mangrove wetlands that have less phosphorus input and lower productivity. All of the riverine sites had TP accumulation rates greater than 0.7 g/m^2/year, with a range from 0.73 to 3.62 g/m^2/year.

Sedimentation and nutrient burial, particularly carbon and nitrogen, in mangrove wetlands include not only allochthonous inorganic matter input (sedimentation) but also net organic matter input resulting from high rates of root production relative to decomposition (Chen and Twilley, 1999). Several studies have found that decay of belowground material is slower than leaf litter (McKee and Faulkner, 2000; Middleton and McKee, 2001; Poret et al., 2007). A large part of sedimentary organic matter in mangrove wetlands is derived from root organic matter (Alongi et al., 2001) and in many forest systems can be the principle source of organic matter in the deeper soil layers (Ludovici et al., 2002). For example, deposition and slow degradation of mangrove roots may contribute more to organic matter accumulation and vertical building of mangrove islands in Belize than total litter fall (Middleton and McKee, 2001; McKee et al., 2007). In carbonate settings, similar to those of south Florida, belowground peat production is the primary control of sediment accretion (Lynch et al., 1989; Parkinson et al., 1994).

Intrasystem nutrient recycling mechanisms (Fig. 7.11) may reduce the loss of nutrients to export and reduce the demand for new nutrients to support primary productivity (Switzer and Nelson, 1972; Turner, 1977; Ryan and Bormann, 1982). The canopy may be a site of nitrogen conservation in mangrove wetlands and, together with leaf longevity, could influence the nitrogen demand of these ecosystems.

It is not clear if the relative amounts of nitrogen conserved in the canopy via retranslocation respond to amount of soil fertility. Another site of nutrient conservation is the forest floor where the concentration of some nutrients in leaf litter during decomposition usually increases on the forest floor (Heald, 1969; Rice and Tenore, 1981; Twilley et al., 1986; Day et al., 1987). If this increase of nutrients, particularly nitrogen, is proportionately greater than the loss of leaf mass during decomposition, then there will be a net input of nitrogen to the forest floor. The source of this nitrogen may be absorption and adsorption processes by bacterial and fungal communities (Fell and Master, 1973; Rice and Tenore, 1981; Rice, 1982), and nitrogen fixation (see discussion above). Twilley et al. (1986) found that this process of nitrogen immobilization occurs in decomposing red mangrove leaf litter in a basin mangrove forest. However, the significance of this ecological process to the nutrient budget of different mangrove wetlands has not been determined.

The atmospheric exchange of carbon from mangrove wetlands has been underestimated based on recent findings associated with sediment remineralization. Total mineralization based on CO_2 fluxes from mangrove sediments is available for a wide range of mangrove systems (Bouillon et al., 2008a). Mangrove creek waters have consistently been found to show high CO_2 oversaturation and hence are a net source of CO_2 to the atmosphere, with an overall average of 59 ± 52 mmol/m^2/ day ($n = 21$) (references from Bouillon et al., 2008a). These sediment and water column estimates relate only to net CO_2 fluxes and not to overall mineralization rates. Up-scaling CO_2 fluxes for sediments and the water column separately is somewhat problematic, since the relative surface areas in these intertidal systems shift during tidal events. Bouillon et al. (2008a) summarized that the similar magnitude in CO_2 efflux from both sediments and water column results in overall CO_2 efflux from mangrove systems to be about 60 ± 45 mmol/m^2/ day (ignoring the CO_2 efflux under light conditions). These CO_2 emission rates are grossly underestimated partially because of the lateral transport of DIC resulting from mineralization of organic rich pore waters that drain from mangrove wetlands. Recent analysis of data sets consistently show that DIC in mangrove creeks far exceeds DOC, by a factor of $\sim$3–10 (Bouillon et al., 2008b). Under the assumption that both originate mainly from the tidal exchange and, therefore, follow the same tidal variations (e.g., Bouillon et al., 2007), this implies that DIC export exceeds DOC export to the same degree. Crab burrows can greatly enhance the surface area of the sediment–air

or sediment–water interface where exchange of CO_2 or DIC can take place, serving as significant conduits for enhancing CO_2 exchange between mangrove sediments and atmosphere (Kristensen, 2008).

These updated estimates of carbon flux from sediments and waters of mangrove wetlands have implications to the debate on how coastal ecosystems influence the global carbon budget (Twilley et al., 1992; Saenger and Snedaker, 1993; Lee, 1995; Duarte et al., 2005; Jennerjahn and Ittekkot, 2002). A reassessment of global mangrove carbon budgets by Bouillon et al. (2008a) estimates that more than 50% of the carbon fixed by mangrove vegetation, estimated $\sim 217 \pm 72$ Tg C/year, appears to be unaccounted for based on estimates of various carbon sinks (organic carbon export, sediment burial, and mineralization). This missing carbon sink is conservatively estimated at $\sim 112 \pm 85$ Tg C/year, equivalent in magnitude to ~ 30–40% of the global riverine organic carbon input to the coastal zone. The analysis above suggests that inorganic carbon flux from sediments and mangrove waters is severely underestimated and that the majority of carbon export from mangrove wetlands to adjacent waters occurs as DIC. Using the average rate of DIC flux above, global levels of CO_2 efflux from both sediments and the water column can be estimated at 42 ± 31 Tg C/year. This analysis suggests that mineralization and export of carbon as DIC is a quantitatively important pathway (178 ± 165 Tg C/year; Bouillon et al., 2008a). The magnitude of this process could be similar to that of the missing carbon sink and may vary in range among different mangrove systems from muddy coasts to carbonate settings.

7.3.4 Mangrove Food Webs

The function of mangrove wetlands as a source of habitat and food to estuarine-dependent fisheries is one of the most celebrated values of forested wetlands (Fig. 7.10). The ''outwelling hypothesis'' of mangrove wetlands has been revised from the original paradigms described by Odum and Heald (1972; see Fig. 7.10) for the estuaries in south Florida. Gut content analyses developed early conceptual models describing how organic detritus from mangrove wetlands dominated the lower level consumers in estuarine food webs (Odum and Heald, 1972, 1975; Yáñez-Arancibia et al., 1988, 1993). These trophic links between mangrove production and higher trophic level consumers were indirect, depending on microbial decomposition of litter fall and consumption by a variety of small detritivores before energy is available to higher trophic level organisms (Hatcher et al., 1989). In addition, surveys of fishery statistics establish a positive correlation between nearshore catch (shrimp or fish) and mangrove area in the vicinity of those harvests (Macnae, 1974; Turner, 1977; Jothy, 1984; Sasekumar et al., 1992; Primavera, 1996). Correlations do not mean causal relationships; however, they show that where extensive mangrove habitats are present, a productive fishery exists; and fisheries in many of these areas consume a substantial amount of detritus in their diets. Such statistics support the claim that the significance of mangrove wetlands to fisheries depends on the total wetland (mangrove) area compared to the water habitats in the region (Twilley, 1995), similar to idea for marshes (Nixon, 1980). In regions with low ratio of wetland to water area, mangrove carbon contribution can range from 2% to 52% of the total available carbon pool for secondary productivity (Twilley, 1988; Wafar et al., 1997; Li and Lee, 1998). Evaluations of different carbon budgets suggest that detritus is an important component of the energy budget of coastal ecosystems depending on the mangrove area/open water area ratio. Other estimates show that large fraction of organic matter produced in mangrove wetlands is buried or consumed by residents of mangrove food webs (Lee, 1990; Robertson et al., 1992; Twilley et al., 1997).

New approaches and techniques using stable isotopes have resulted in a great deal of ambiguity on specific conclusions associated with coastal food webs (Rodelli et al., 1984; Newell et al., 1995; Primavera, 1996; Lonnergan et al., 1997; Cifuentes et al., 1996; Bouillon et al., 2002; Hsieh et al., 2002; Schwamborn et al., 2002). At present, stable isotope techniques do not show a strong direct connection between mangrove wetlands and food webs as has been suggested by gut content, fishery statistics, or organic matter mass balances. The dual-gradient concept of detritus transport in estuaries (Odum, 1984) states that organic carbon distributions occur along two gradients, salinity axis and marsh stream order. According to the dual-gradient concept of detritus transport, isotopic ratios between particulate organic carbon and consumer tissues will change from predominantly terrestrial material to predominantly phytoplankton (less negative) as salinity increases. There is also a shift from mangrove carbon or benthic microalgae to predominantly phytoplankton carbon along increased stream orders. Low stream orders with high wetland/open water ratio are more apparent in the oligohaline and mesohaline regions of the estuary than in polyhaline regions at the mouth of the estuary (Odum, 1984). In these small streams, where high exchange of organic matter and nutrients between water bodies and surrounding wetlands is expected, different groups of consumers may interact to move intertidal production horizontally across landscape

boundaries. Such classification seems to be a very appropriate guide in the analysis and interpretation of mangrove detritus as energy source, and this typology as a frame of reference is similar to the conceptual model that isotopic signature of mangrove carbon will vary among distinct ecogeomorphic settings (Twilley, 1995).

The secondary productivity of tropical estuarine fishes in mangrove wetlands have three contributions to the energy and nutrient dynamics of estuarine ecosystems: (i) they can be stores of nutrients and energy, (ii) they control rates and magnitude of energy flow through grazing of food sources, and (iii) they move energy and nutrients across ecosystem boundaries (Yáñez-Arancibia, 1985). The migratory nature of many of the nekton communities and the seasonal pulsing of both organic detritus input and primary productivity result in very complex linkages of forested wetlands with estuarine-dependent fisheries (Fig. 7.10). The sequential pulsing of primary production by planktonic and macrophyte communities coupled with seasonal export of mangrove detritus suggest that the delivery of organic matter sustains high estuarine secondary production and species diversity of estuarine-dependent consumers (Fig. 7.10) (Rojas-Galaviz et al., 1992; Yáñez-Arancibia et al., 1993). The seasonal coupling of primary and secondary production in mangrove ecosystems, along with variation in environmental conditions, shows how the functional assemblages of fish use tropical lagoon habitats in time and space to reduce the effect of competition and predation. Assemblages of macroconsumers within functional groups play an important ecological role by coupling life history strategies with the environmental gradients within the estuary. There are two main mangroves habitats, the fringe (SMS) and riverine (FLS), where the same fish population assemblages utilize the habitats in a sequential manner from one season to the next. This diversity in behavior suggests that the lag in fluctuations of total biomass through the year, as is common in high latitude estuaries, is a consequence of the sequential use of the different mangrove habitats by different species (seasonal programming). Although common species appear in fringe and riverine mangroves, there are different peaks of abundance regulated by climatic changes that control the biological and physical characteristics of the two habitats (Yáñez-Arancibia et al., 1988, 1993). Thus the dominant species (or keystone species) act as controllers of the structure and function of the whole macroconsumer community, while the physical variability and mangrove productivity modulate their species diversity. The seasonal nature of these processes secures the recruitment and functional species diversity of estuarine nekton communities (Yáñez-Arancibia et al., 1993).

7.4 HUMAN IMPACTS AND MANAGEMENT

The ecological properties of mangrove wetlands described in the previous section define the function of these ecosystems in productivity, biogeochemistry, and food webs of mangrove-dominated estuaries. Such functions determine the ecosystem services of mangrove wetlands such as controlling water quality, providing habitat value, stabilizing shore lines, and reducing risks from storm surge. Mangrove wetlands produce a variety of forest products, support the productivity of economically important estuarine-dependent fisheries, and modify the water quality in warm temperate and tropical estuarine ecosystems. Because of the value of these ecosystem services in many coastal settings, there is an increased human utilization of mangrove resources that vary throughout the tropics depending on economic and cultural constraints (Fig. 7.13). Economic constraints are usually in the form of available capital to fund land-use changes in coastal regions, as well as river basin development (Twilley et al., 1998). Cultural constraints are complex and determine the degree of environmental management and natural resource utilization. However, the sustainable utilization of coastal resources is, to a large degree, controlled by these two social conditions of a region. Human use and value of mangrove wetlands are therefore a combination of both the ecological properties of these coastal ecosystems together with patterns of social exploitation. Therefore, any best management plan designed to provide for the sustainable utilization of mangrove wetlands has to consider both the ecological and social constraints of the region. Humans are part of all ecosystems, and management of natural resources is a combination of policies that seek to regulate the actions of societies within limitations that are imposed by the environment.

The utilization of mangrove resources by humans can have negative feedback effects on the ecological processes of mangrove ecosystems (Twilley et al., 1998; Fig. 7.13). These feedbacks can be indirect impacts such as diversion of freshwater, which can cause changes in the productivity, litter export, and biogeochemistry of mangrove wetlands, among other processes. Direct impacts may include inputs
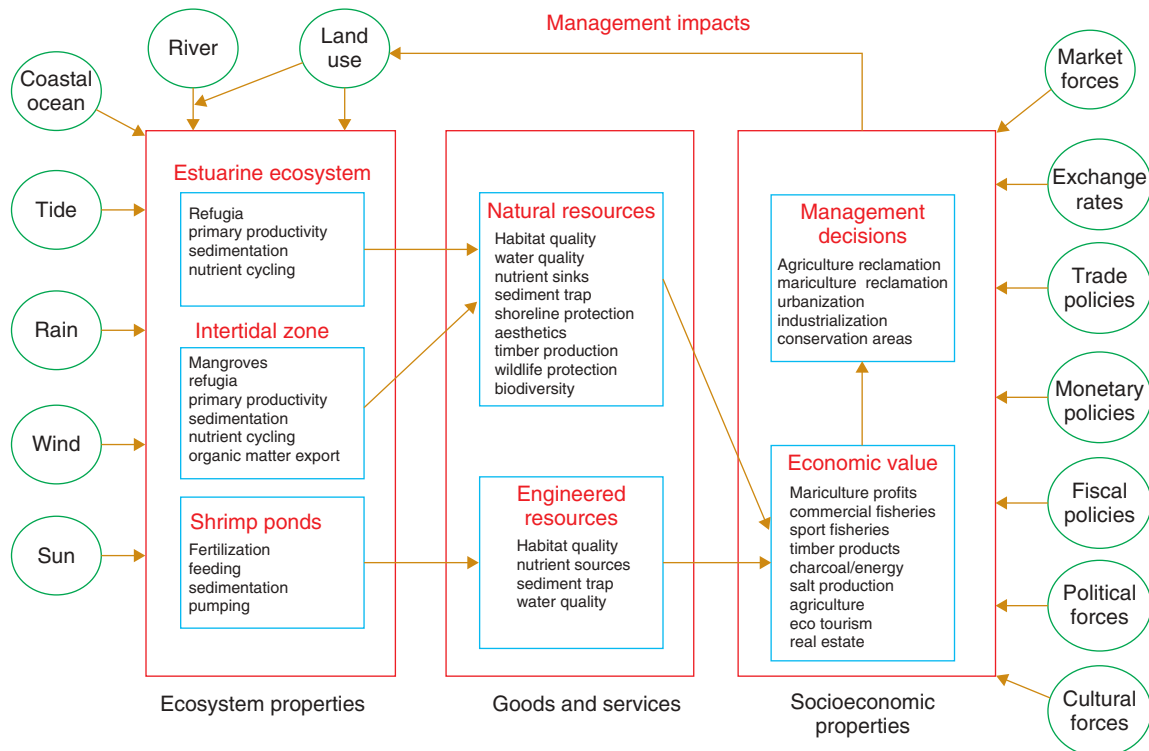
FIGURE 7.13 Diagram of the linkages among environmental setting, ecosystem properties, ecological functions, and uses of mangrove ecosystems, including feedback effects of human utilization on ecosystem properties. *Source:* Modified from Twilley (1995).

of excess nutrients or toxic substances such as oil that limit the ecological processes of mangrove wetlands. If these impacts limit the ecological processes and thus the function of mangrove wetlands, then the impact connects all the way back to the use and value of these natural resources. Thus the properties of mangrove wetlands are influenced by both the environmental constraints (forcing functions in Fig. 7.13) and the social constraints (economics and culture in Fig. 7.13) of a coastal region. Environmental and social constraints of mangrove wetlands are inextricably linked by the nature of environmental feedbacks from human exploitation. Thus the ecology of mangrove wetlands has to include the impacts of humans and nature. Sustainable development of mangrove wetlands may be viewed as the proper balance between environmental and social constraints that allow for the continued use and value of these coastal resources by future generations.

Deforestation of mangrove wetlands is associated with many uses of coastal environments including urban, agriculture, and aquaculture reclamation, as well as the use of forest timber for furniture, energy, chip wood, and construction materials (Watson, 1928;

Saenger et al., 1983). In the Gulf of Mexico and Caribbean, there are very few examples of mangrove use in silviculture as throughout most of the Neotropics, in comparison to Indonesia where mangrove plantations have been in existence for several decades (Watson, 1928; Snedaker, 1986). Two reclamation activities that have contributed to examples of massive mangrove deforestation are agriculture and aquaculture enterprises. Agriculture impacts to mangrove wetlands are most noted in West Africa and parts of Indonesia (Ponnamperuma, 1984), but there is little direct reclamation of mangrove intertidal areas for rice production in the Neotropics. Many of the large agricultural uses are found in humid coastal areas or deltas where freshwater is abundant and intertidal lands are seasonally available for crop production. Mariculture use of the tropical intertidal zones has become one of the fastest growing aquaculture industries in the past decade. One of the largest and most publicized is the expansion of shrimp farming in Ecuador, where in the late 1980s, there were more shrimp produced in the ponds of this Pacific coastal zone than anywhere else in the world (Twilley et al., 2000). The environmental impact of shrimp farming on mangrove wetlands and water quality of

tropical estuaries may threaten the sustainability of this economic activity (Twilley et al., 1998, 2000).

Human alterations of upland watersheds causing diversion of freshwater (dams and canals) can have severe impacts on coastal forested wetlands, particularly in dry coastal environments. Regional scale changes in freshwater surface inflow into coastal areas can alter the landscape distribution of mangrove wetlands and reduce the productivity and habitat quality of these forested wetlands. Together, these disturbances can alter the secondary productivity of tropical estuarine ecosystems because of degradation of habitat and environmental quality and alter the terrestrial and aquatic food webs that mangrove ecosystems support. The most dramatic impact of freshwater diversion in the Neotropics has been documented in Colombia, where the construction of highways and levees restricted the flow of the Magdalena River to the Cienaga Grande de Santa Marta resulting in the death of nearly 25,000 ha of mangrove wetlands over the past decade (Botero, 1990; Twilley et al. 1999a; Rivera-Monroy et al., 2011). The sensitivity of mangrove wetlands to slight changes in freshwater input in dry coastal regions that dominate the Caribbean and most of the Gulf coast has been well documented (Cintrón et al., 1978).

Other human impacts on mangrove wetlands can be more direct such as the introduction of contaminants that can disrupt the natural ecological processes of these forested wetlands (Fig. 7.13). Deterioration of water quality includes inputs of excessive nutrients to coastal waters (eutrophication) and toxic materials (heavy metals, oil spills, and pesticides). The increased attraction of coastal environments by humans has made coastal regions more vulnerable to these water quality problems. The increase in residential and recreational real estate in coastal regions not only causes direct impacts such as deforestation, but this land use also increases the amount of nutrient discharge to coastal waters. A recent study of mangrove wetlands in Puerto Rico has demonstrated the negative and positive impacts of human activities on mangrove wetlands over a period of 200 years (Martinuzzi et al., 2009). During the period 1800–1940, the agricultural and urban expansion within the island caused a 45% decline in mangrove cover (from 12,000 to 6500 ha), mostly due to changes in hydrology, drainage, or excessive sedimentation. After late 1940 with the onset of the industrial economy, mangrove forests expanded by natural recovery due to reduced land-use pressure. Nevertheless, between 1960 and 1970 mangrove land cover decreased due to urban expansion. Since the establishment of legal protection for all mangrove wetlands in the early 1970s, reductions in area have been prevented in spite of continuing urbanization.

Mangrove wetlands have the potential to be used in a landscape design to remove excess nutrients from wastewaters before they are discharged to coastal systems. This potential depends on the nutrient biogeochemistry described above such that the nutrient sink capacities of mangrove wetlands are optimized relative to the nature of the input. There have been some descriptions of how to use mangrove wetlands for the use of nutrient abatement in wastewaters (Clough et al., 1983; Breaux and Day, 1999). As described above, mangrove wetlands have a high capacity of nitrogen removal via denitrification (Nedwell, 1975; Corredor and Morell, 1994), and nutrient burial in mangrove soils may also be an important nutrient removal process. But the detail designs of hydrology and environmental engineering to optimize for these losses need better specifications, since there are a few pilot studies of these operations (Twilley et al., 1999b; Rivera-Monroy et al., 1999). This management approach using the nutrient biogeochemistry of mangrove wetlands represents a very important point in the management of these coastal forests (Fig. 7.13); that the natural free services of these forested wetlands as a nutrient sink can minimize environmental impacts. Engineering mangrove wetlands for the use of waste water treatment rather than removing these forested wetlands can be a positive feedback to sustain human activities in the coastal zone.

Oil spills represent contaminants to mangrove wetlands that can alter the succession, productivity, and nutrient cycling of these coastal forested wetlands. These impacts have been well documented in ecological studies in Puerto Rico (Cintrón et al., 1981), Panama (Duke and Pinzon, 1993; Garrity et al., 1994 and citations within), and Gulf of Mexico (Getter et al., 1981). Negative feedbacks of contaminants such as oil in tropical coastal waters are the products of both oil exploration and transportation. These inputs become constraints on the ecological processes of mangrove wetlands by limiting their ability to support ecological functions that provide ecosystem services in tropical coastal regions, such as fisheries and forestry. Efforts to minimize the damage of oil spills and enhance the recovery of mangrove wetlands are important to minimize the complex loss of ecological functions to the coastal zone. An oil slick in a mangrove wetland will cause a certain mortality of trees depending on the concentration of hydrocarbons and species of trees, as well as the edaphic stress levels already existing at the site (Duke and Pinzon, 1993; Cintrón et al., 1981). Thus, those mangrove wetlands in dry coastal environments may be more

vulnerable to oil spills than those in more humid environments. In addition, Duke and Pinzon (1993) found that the exposure of the shore to wind and wave energy was an important factor in determining the degree of tree mortality and reductions in growth.

7.5 CONSERVATION AND MANAGEMENT

Mangrove ecosystems support a variety of marine and estuarine food webs involving an extraordinarily large number of animal species (Odum and Heald, 1972; Yáñez-Arancibia et al., 1988; Thayer et al., 1987; Gilmore and Snedaker, 1993) and complex heterotrophic microorganism food web (Odum, 1971; Fell and Master, 1973; Snedaker, 1989; Robertson et al., 1992). In the new world tropics, extensive surveys of the composition and ecology of mangrove nekton have found 26–114 species of fish (from Table 9 in Robertson and Blaber, 1992). In addition to the marine and estuarine food webs and associated species, there are a relatively large number and a variety of animals that range from terrestrial insects to birds that live in and/or that feed directly on mangrove vegetation. These include sessile organisms such as oysters and tunicates, arboreal feeders such as foliovores and frugivores, and ground-level seed predators. Sponges, tunicates, and a variety of other forms of epibionts on prop roots of mangroves are highly diverse (Sutherland, 1980; Rützler and Feller, 1988; Ellison and Farnsworth, 1992), especially along mangrove shorelines with little terrigenous input. There are four distinct spatial guilds of residents and casual faunal populations in south Florida mangroves that may have well over an estimated 200 species, many of which are as yet uncataloged (Gilmore and Snedaker, 1993). In addition, over 200 species of insects have been documented in mangrove wetlands in the Florida Keys (Simberloff and Wilson, 1969). This same richness of insects and faunal biota has been observed in other parts of the Caribbean (Rützler and Feller, 1988; Bacon, 1990; Farnsworth and Ellison, 1991, 1993).

One of the most published links between mangrove biodiversity and ecosystem function may be the presence of crabs in mangrove wetlands (Jones, 1984; Smith, 1987; Twilley et al., 1997). In general, the mangrove crab fauna is dominated by representatives of two families, the Ocypodidae and Grapsidae, and each family by one genus, *Uca* and *Sesarma*, respectively. Furthermore, within the Grapsidae, the genus *Sesarma* accounts for over 60 species of crabs

predominantly associated with mangrove wetlands (Jones, 1984), of which the tropical Americas have only 3–5 species compared to over 30 in other tropical continents. Crabs can influence forest structure (Smith, 1987; Smith et al., 1989; Robertson et al., 1990), litter dynamics (Robertson and Daniel, 1989), and nutrient cycling (Smith et al., 1991) of mangrove wetlands, suggesting that they are a keystone guild in these forested ecosystems. The selective consumption by crabs on mangrove propagules influences rates of sapling recruitment by removing some species from zones of crab habitation, although this process seems to be less significant in the Gulf of Mexico wetlands than in Australia (Smith et al., 1989). In the Neotropics, crab consumption is less intense and recruitment generally follows the distribution patterns of propagules and the constraints of edaphic conditions.

The fragmentation of mangrove-dominated landscapes is believed to create the same types of problems for migratory organisms that are associated with the fragmentation of upland forests, yet there has been little, if any, research on this topic. There is no documentation concerning diel or seasonal migration patterns of resident species within mangroves, or how such species might be affected by the impact of fragmentation. For instance, sea grass and adjacent mangrove habitats are used by many species of nekton and are generally characterized by high fish abundance and diversity. It is clear that the utilization of the two interacting habitat by fishes is spatially distinct but linked by the life cycles of organisms (Yáñez-Arancibia et al., 1993). There is a strong correlation between the life history patterns of migratory fish and the pattern of primary production, using the two habitats sequentially in a time period. The fragmentation of mangrove-sea grass landscapes probably will reduce ecosystem complexity and nekton diversity. It has been speculated that one of the consequences in loss of mangrove area and/or increased fragmentation will be reduction in population numbers (and this may be important for commercial species) or outright local extinctions of certain species. However, as reviewed by Robertson and Blaber (1992), there is no empirical evidence that such a consequence will occur.

Restoration of ecosystems is considered the ultimate test of our scientific understanding of the ecological processes that control the structure and function of the landscape (Ewel, 1987). There have been several reviews of mangrove restoration (Lewis, 1982; Field, 1996), and collectively that have alluded to the concept that since these forested wetlands are adapted to stressed environments, they are relatively

amenable to restoration efforts. The success of mangrove restoration is the establishment of the proper environmental settings that have been described in this chapter that control the characteristic structure and function of mangrove wetlands. Degraded or disturbed mangrove wetlands can be described as a divergence in mangrove structure and function away from the natural or reference condition (reference site). The degree of this divergence in some selected properties of the degraded site away from the natural site depends on the magnitude of the impact. The goal of ecological restoration is to return the degraded site back to either the natural condition (restoration) or to some other new condition (rehabilitation). In most cases, the damage to mangrove environments is so severe that restoration efforts are no longer available. The rates of change in the ecological characteristics of mangrove wetlands between natural, degraded, and some rehabilitated condition are known as *trajectories*. The nature of these trajectories will depend on the type of environmental impact, the magnitude of the impact, and the ecogeomorphic type of mangrove wetland that is impacted. Alterations in the environmental setting have to be restored or maintained to obtain a restoration trajectory whereby a degraded site returns back to a natural condition; deviations in the environmental settings will more likely result in some altered or rehabilitated mangrove wetland. Trajectories are a very important concept in the ecological restoration of any ecosystem, since they include both the structural and functional characteristics of the sites relative to natural conditions and the time required to obtain a rehabilitated state or condition (Twilley et al., 1999a).

The effectiveness of any mangrove restoration project depends on the establishment of proper site conditions including currents from waves and winds, tidal flooding frequency, temperature, soil resources, and regulators (salinity and hydrogen sulfide), along with ecological processes of the site such as the availability of propagules and the recruitment of these individuals to sapling stage of development. Thus, the seasonal nature of planting and propagule density, along with increased selective mortality of propagules from physiological stress, increased mortality by crab consumption and disease, will establish the initial trajectory of any restoration project (Twilley et al., 1999a). Some of the key parameters of a restoration project include the elevation of the landscape to provide the proper hydrology of the site, recognizing the significance of natural processes to sustaining the restored condition, and proper planting techniques to enhance recruitment (Bosire et al., 2008).

There are several examples of mangrove restoration projects in Florida and Puerto Rico that include some recommendations concerning site preparation and mangrove planting techniques (see references in Lewis, 1990a,b; Cintrón, 1990; and Snedaker and Biber, 1996). The lack of postproject monitoring has limited the ability to determine what specific techniques deliver the optimum results. Recent studies on factors that affect tolerance of seedlings to environmental and ecological processes discussed above provide more specific information on the nature of site preparations needed to establish mangrove forests (Bosire et al., 2008).

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CHAPTER EIGHT

ESTUARINE BENTHIC ALGAE

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8.1 INTRODUCTION

Benthic algae play a key role in regulating carbon and nutrient turnover and in supporting food webs in shallow-water coastal environments. They are especially important in the wide diversity of estuarine habitats found worldwide. Benthic producers are generally divided into macroalgae and microalgae (also known as *microphytobenthos*). Macroalgae contribute between 4.8% and 5.9% of the total marine net primary productivity (calculated from Duarte and Cebrian, 1996). Although lower than total oceanic (81.1%) and coastal (8.5%) phytoplankton, the local macroalgal productivity (per square meter) is comparable to some of the most productive terrestrial ecosystems such as tropical forests. Benthic microalgae often form visible brown or green mats on the sediment surface. These mats are thin, as the microalgae are confined to the photic zone (1–3 mm) of the sediment, yet the density of algae and other microorganisms is usually high, often 100–1000 times higher than in the water column. In shallow estuaries, benthic microalgae normally account for 20–50% of the total primary production (Underwood and Kromkamp, 1999). In this chapter, we discuss the benthic algal communities that inhabit the soft-bottom (mud/sandflat, seagrass bed, marsh), hard-bottom (rocky intertidal, shallow subtidal), and coral reef habitats that lie within estuarine ecosystems.

8.2 TAXONOMY

All algae at some stage of their life cycles are unicellular (usually as reproductive stages such as spores or zygotes), and they are viewed as ''primitive'' photosynthetic organisms because of their relatively simple construction and their long evolutionary history. Prokaryotic ''blue-green algae,'' or cyanobacteria, are the oldest group, with fossils dating back almost 3000 million years. These first algal fossil remains include stromatolites, which are structures formed in shallow tropical waters when cyanobacterial mats accrete layers by trapping, binding, and cementing sediment grains. Photosynthesis by these early primary producers was responsible for much of the oxygen that eventually built up to the levels that occur today. Evolution of eukaryotic algae occurred much later, about 700–800 million years ago, although this date is difficult to determine more exactly as most groups were composed of soft tissue that would not have been preserved reliably in the fossil record.

Marine macroalgae or ''seaweeds'' are a functional rather than phylogenetic group comprising members from two kingdoms and at least four major phyla (divisions). There is a wide variation in algal classification schemes among systematists, but the traditional divisions for macroalgae are *Cyanobacteria* (prokaryotic blue-green algae, sometimes termed

Cyanophyta), *Chlorophyta* (green algae), *Phaeophyta* (brown algae), and *Rhodophyta* (red algae) (Littler and Littler, 2000).

Marine green algae range from cold temperate to tropical waters. Green algae reach highest diversity and abundance in tropical regions, with several families such as the *Caulerpaceae* and *Udoteaceae* being very abundant in coral reef and associated seagrass habitats. Often overlooked, but very abundant, are filamentous green algae that bore into coral skeleton and proliferate widely, with high rates of productivity (Littler and Littler, 1988). Opportunistic green algae form nuisance blooms in estuaries worldwide; in eutrophic systems, they form almost monospecific mats of extremely high biomass.

Brown algae are almost exclusively marine and are dominant in temperate waters where hard-bottomed habitats occur. Some genera of structurally robust forms such as *Laminaria* and *Sargassum* dominate in very high energy zones. Kelps are ''ecoengineers'' that form extensive forests in coastal areas where nutrients are supplied by upwelling. Other groups of fast growing and more opportunistic genera such as *Dictyota* may form seasonal blooms in tropical and subtropical regions.

The majority of seaweed species is in the *Rhodophyta*. At present, the approximately 4000 named species of red algae exceed the number of species in all other groups combined (Lee, 1999). Although red algae are extremely speciose in tropical and subtropical regions, their biomass is low relative to that in temperate areas. The most common forms of red algae in the tropics include crustose members of the family *Corallinaceae* as well as a high diversity of small, less obvious filamentous species that comprise algal turfs. However, there are some genera of upright and branching calcifying forms such as *Galaxaura* and branching or flattened foliose red algae in the genera *Laurencia, Asparagopsis*, and *Halymenia* that can be quite conspicuous and abundant on reefs under certain conditions. The highest biomass of red algae is found in temperate and boreal regions. Some large fleshy members of the *Rhodophyta* with descriptive names such as ''Turkish towels'' blanket rocky intertidal and subtidal regions. Other genera, such as *Gracilaria*, form blooms in estuaries and lagoons.

In most cases, the benthic microalgal community in estuarine habitats is a mixture of several taxonomical groups, although blooms tend to be dominated by one or few species. The taxa that form typical visible microbial mats on the sediment surface in the photic zone are mostly diatoms (phylum *Bacillariophyta*) and cyanobacteria (the prokaryotic phylum *Cyanophyta* or *Cyanobacteria*). The term microbial mat originally

referred to consortia dominated by prokaryotic phototrophs (Stal and Caumette, 1992), but here it is used in a broader sense, including all types of mats consisting of microscopic phototrophic organisms.

Diatoms are by far the most common taxonomic group, giving the sediment a brown color because of the pigment fucoxanthin. Benthic diatoms are different from planktonic diatoms in that they mostly represent the pennate diatoms, with more or less bilateral symmetry (classes *Fragilariophyceae* and *Bacillariophyceae*; according to the systematics in Round et al., 1990). They are solitary, and when they have a raphe (a slitlike structure) on both valves of their silica frustule (or covering), they are motile. Those that have no raphe, or a raphe only on one valve, can form short colonies. Some centric diatoms (class *Coscinodiscophyceae*) can be common on sediments, for example, *Paralia sulcata*. The size of benthic diatoms ranges from a few micron to 500 μm; the sigmoid cells belonging to the genera *Gyrosigma* and *Pleurosigma* are some of the largest. Because many benthic diatoms are small (<10 μm), it is difficult to identify live cells to species level in a light microscope. When the organic cell contents are removed by oxidation to prepare ''diatom slides,'' the taxonomically important ornamentation of the silica frustule can be viewed.

Cyanobacteria are widespread both on soft and hard substrates. They form mats along reef margins or on coral (Smith et al., 2009), may be epiphytic on other algae (Fong et al., 2006), rapidly colonize open space opportunistically after disturbances (Belk and Belk, 1975), and may bloom in response to nutrient enrichment (Armitage and Fong, 2004). Cyanobacterial mats are also common on salt marshes, particularly in subtropical and tropical estuaries and extreme habitats such as hypersaline lagoons. They are laminated systems that form interdependent layers of vertically stratified phototrophic, heterotrophic, and chemotrophic microorganisms. They function as laterally compressed ecosystems that support most of the major biochemical cycles within a vertical dimension of a few millimeters (Paerl and Pinckney, 1996). Typical benthic genera are the filament-forming *Oscillatoria* and *Microcoleus* and the colony-forming *Merismopedia*. Many filamentous benthic cyanobacteria fix nitrogen gas (N_2) (Paerl and Pinckney, 1996). See Chapter 4.

Flagellates such as dinoflagellates (*Dinophyta*), euglenophytes (*Euglenophyta*), chlorophytes (*Chlorophyta*), and cryptophytes (*Cryptophyta*) are also found in estuarine microphytobenthos. Dense populations of dinoflagellates of the genus *Amphidinium* can occasionally give the sediment surface a red brown

color. See Chapter 4. As for phytoplankton, photopigments can be used to identify and quantify the presence of major taxonomical groups of benthic microalgae in surface sediments (Chapter 4).

8.3 FUNCTIONAL FORMS

Structurally, benthic algae include diverse forms that range from single cells to giant kelps over 45 m in length with complex internal structures analogous to vascular plants. Species diversity may be extremely high in benthic algal communities (Guiry and Guiry, 2007; see http://www.algaebase.org), and can be simplified by classifying algae by functional-form categories. Steneck and Dethier (1994) classified algae into the following groups based on productivity and susceptibility to grazing: microalgae, filamentous, crustose, foliose, corticated foliose, corticated macrophyte, leathery macrophyte, and articulated calcareous.

For macroalgae, a classification scheme based on a broader set of characteristics was put forward by Littler and Littler (1984): sheet, filamentous, coarsely branched, thick leathery, jointed calcareous, and crustose forms (Table 8.1). These groups of functional forms have characteristic rates of nutrient uptake and mass-specific productivity, turnover rates, and resistance to herbivory that allow them to perform similarly in response to environmental conditions, despite differences in taxonomy. A key characteristic that drives these differences in function based on form is the ratio of surface area to volume ($SA{:}V$) of the

thallus. Macroalgae are also grouped more generally into "ephemeral" or "perennial" forms. Ephemeral macroalgae typically have a high thallus $SA{:}V$ and inherently rapid nutrient uptake and growth rates. Most of the bloom-forming macroalgae that occur in response to nutrient overenrichment (eutrophication) (e.g., *Ulva* sp., *Chaetomorpha* sp., *Gracilaria* sp., *Polysiphonia* sp.) are ephemeral, and usually comprise very simple thallus forms such as those in the first three categories of Littler and Littler (1984). They tend to live floating and unattached or loosely attached to hard surfaces (i.e., shells, worm tubes) on the sediment (Schories and Reise, 1993; Thomsen and McGlathery, 2005). Perennial species such as crustose and calcareous macroalgae tend to live in low nutrient or stressful habitats (e.g., low light, low temperature) where a slow growth rate or perennial life form confers an advantage.

For benthic microalgae that live in sediments, the energy regime of the habitat determines the dominant life forms. In wave-exposed, well-sorted sands, life forms that are firmly attached to sand grains dominate and are called *epipsammic* (attached to sand grains). In high energy sand, most epipsammic diatoms are found in the crevices of the sand grains, where they are protected from abrasion. Typical genera are *Achnanthes, Cocconeis* (with raphe on one valve), and small-sized *Navicula*-like genera and *Amphora* (raphe on two valves) (Fig. 8.1a). These life forms attach by mucopolysaccharides extruded through their raphe. In less wave-exposed sands, solitary cells or colonies

TABLE 8.1 Functional-form groups of predominant macroalgae, their characteristics, and representative taxa

	Functional-form Group	External Morphology	Comparative Anatomy	Thallus Size/texture	Example Genera
1.	Sheetlike algae	Flattened or thin tubular (foliose)	One–several cell layers thick	Soft, flexible	*Ulva* *Halymenia*
2.	Filamentous algae	Delicately branched	Uniseriate, multiseriate, or lightly corticated	Soft, felxible	*Chaetomorpha* *Cladophora*. *Gelidium* *Caulerpa*
3	Coarsely branched algae	Terete, upright, thicker branches	Corticated	Wiry to fleshy	*Acanthophora* *Laurencia*
4.	Thick leathery macrophytes	Thick blades and branches	Differentiated, heavily corticated, thick walled	Leathery-rubbery	*Sargassum* *Turbinaria*
5.	Jointed calcareous algae	Articulated, calcareous, upright	Calcified genicula, flexible intergenicula	stony	*Galaxaura* *Amphiroa*
6.	Crustose algae	Epilithic, prostrate, encrusting	Calcified, heterotrichous	Stony and tough	*Porolithon* *Hydrolithon*

Source: Adapted from Littler and Littler (1984).
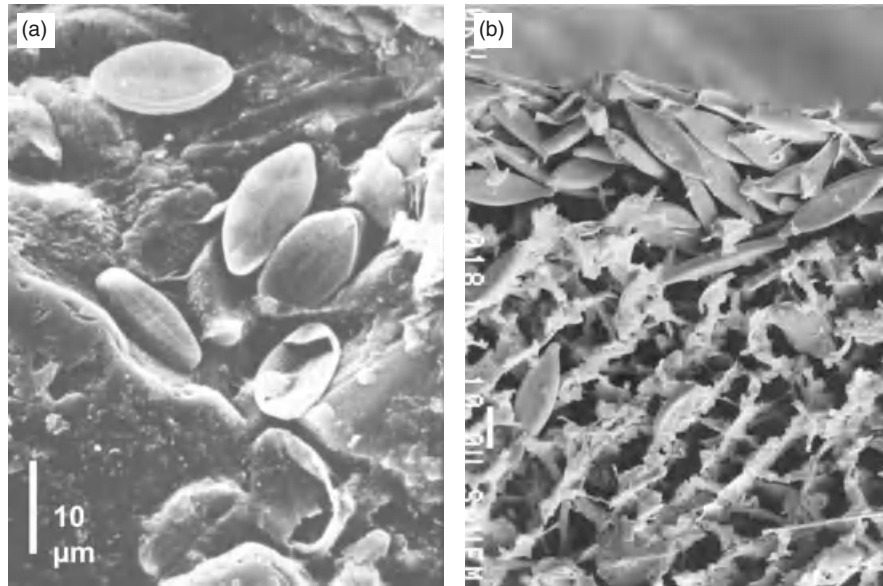
FIGURE 8.1 Benthic diatom assemblages viewed by scanning electron microscopy (SEM). (a) Epipsammic diatoms (*Achnanthes* and *Navicula*) in the cavity of a sand grain. (b) Vertical cut of a sediment surface at low tide photographed in a low temperature SEM. Motile diatoms have moved to the sediment surface where they form a dense microalgal mat. Strings forming networklike patterns consist of extracellular polymeric substances (EPS) excreted by diatoms (the pattern is an artifact produced by the method). *Source:* Photograph (a) by H. Håkansson and K. Sundbåck, (b) by A. Miles, Sediment Ecology Research Group, University of St. Andrews, Scotland.

of small diatoms are found protruding from the sediment particles. Such genera include *Fragilaria* and *Opephora*, which lack raphe, but attach through a mucopolysaccharide pad extruded from apical pores. The more sheltered the sediment is from wave exposure, the more common are motile life forms (*epipelic*; originally meaning ''living on mud''). These are the diatoms that form visible, cohesive microbial mats on the sediment surface, particularly on muddy tidal flats (Fig. 8.1b). The cohesiveness is due to extracellular polymeric substances (EPS) that are extruded from the raphe and from pores in the silica frustule. The production of EPS is related to the motility of raphe-bearing life forms (genera such as *Navicula, Amphora, Nitszchia, Gyrosigma*, etc.; for systematics of the diatom genera, see Round et al., 1990). In fine sediments, epipsammic life forms are found attached to flocs of organic matter consisting of detritus and fecal pellets.

8.4 HABITATS

8.4.1 Soft-Bottom: Mud/Sandflats, Seagrass Beds, and Marshes

Benthic algae are important members of the primary producer community in shallow soft-sediment systems worldwide where light penetrates to large areas of the benthos. In those systems subject to low nitrogen loading rates, macroalgae occur in relatively low abundance attached to the benthos, are epiphytic on seagrass blades, or form drifting mats. Within tropical seagrass beds, calcareous and/or siphonaceous green macroalgae such as *Halimeda* and *Caulerpa* are commonly attached to the benthos; calcification and chemical defenses provide protection from most herbivores. Calcified macroalgae ultimately contribute significantly to the accumulation and stabilization of tropical sands (MacIntyre et al., 2004). In both tropical and temperate seagrass beds, macro- and microalgae attach epiphytically to seagrass blades. Although even low abundances of epiphytes can have negative effects on seagrasses due to shading and interference with gas and nutrient exchange, in seagrass systems with low nutrient loading and intact herbivore populations epiphyte biomass accumulation is modest and contributions to food webs are significant (Williams and Ruckelshaus, 1993). In low nutrient soft-sediment systems, drift macroalgae are also present in low abundance, but are ecologically important as they may provide protection from predation and aid in dispersal of invertebrates and fishes (Salovius et al., 2005; Holmquist, 1994). However, when abundances increase, drifting mats can have negative effects on

their seagrass hosts, reducing density through smothering and shading (Huntington and Boyer, 2008).

Macroalgae can occasionally be abundant in the lower salt marsh zone in estuaries. Examples include the ephemeral green algae (*Blidingia*, *Rhizoclonium*, and *Ulva* (including former *Enteromorpha*)), slow-growing stress tolerant and long-lived brown algae (*Fucus* and *Ascophyllum*), inconspicuous slow-growing red algae (*Bostrychia* and *Caloglossa*), and invasive species (e.g., *Gracilaria vermiculophylla*). Many macroalgae in the understory of salt marsh vegetation are complexed with cyanobacteria and diatom mats. Productivity of these mixed algal communities can be very high, at times equaling or exceeding the productivity of the vascular plant canopy (Zedler, 1982). When algae are abundant in the understory of the vascular plant community, they may affect primary production rates, biogeochemical cycling, trophic interactions, and environmental conditions, such as evapotranspiration, infiltration, and sediment characteristics (Brinkhuis, 1977; Moseman et al., 2004; Boyer and Fong, 2005; Thomsen et al., 2009).

Similar to macroalgae, benthic microalgae are also important primary producers on illuminated shallow-water sediments. On sediments where there are no macroscopic primary producers, they are the only benthic primary producers, forming the base for benthic food webs. Benthic microalgae are most well studied on tidal mud- and sandflats, but are also important in subtidal habitats, particularly in microtidal estuaries, where the water column often stays clear through most of the day because of the lack of strong tidally induced turbidity. In large deep estuaries, such as Chesapeake Bay, a high percentage of the sea floor is within the photic zone, enabling primary production to occur over large areas.

8.4.2 Hard-Bottom: Rocky Intertidal, Shallow Subtidal

Rocky intertidal and shallow subtidal zones worldwide are dominated by macroalgae, microalgae, and sessile invertebrates. While common along open coasts, some rocky areas exist in sheltered estuarine systems such as fjords and sounds. The rocky intertidal zone is characterized by environmental extremes (temperature, salinity, desiccation, nutrient supply), yet there are also strong biotic interactions that combine to produce striking patterns of zonation along elevational gradients. Both macroalgae and microalgae play important roles as *in situ* producers, forming the base of local food webs.

Macroalgae in rocky intertidal habitats are highly diverse and abundant, especially in temperate regions. Virtually every functional form of macroalgae can be found in hard-bottomed habitats, from delicate branching genera such as *Plocamium* to large and fleshy reds and browns such as *Mastocarpus* (Turkish Towel) and *Egregia* (Feather Boa Kelp). Many classical studies have identified the importance of top–down forces in controlling the structure of rocky intertidal communities (e.g., Connell, 1972; Paine, 1974). More recent work has begun to focus on bottom–up processes as well as the relationship between biodiversity and ecosystem functions such as productivity and nutrient retention (e.g., Worm and Lotze, 2006; Bruno et al., 2008). Although rocky intertidal and shallow subtidal systems in tropical regions are far less studied, there is some evidence to suggest that macroalgal communities in some areas, such as the Pacific coast of Panama, are controlled by the same ecological processes as temperate systems (Lubchenco et al., 1984). In polar regions, the extreme and variable light climate and continuous near-freezing temperatures impose constraints on macroalgal production and depth distribution, as areas are typically ice covered for all but two months of the year. Despite these harsh conditions, crustose coralline macroalgae can be found down to 50 m depth in Arctic estuaries where the light level is only 0.004% of surface irradiance (Rysgaard et al., 2001). Large brown algae in the genera *Laminaria* and *Fucus* are often the community dominants in the 2–20-m-depth region attached to rocks, stones, and even gravel in protected areas (Witman and Dayton, 2001; Krause-Jensen et al., 2007). Physical disturbance by ice scouring often limits the distribution at shallow depths, and light limitation and possibly also disturbance from walrus feeding activities sets the lower limit of distribution in Arctic waters (Borum et al., 2002; Krause-Jensen et al., 2007).

Although macroalgae are the most prominent vegetation of rocky shores, there is also another less evident, but ecologically important algal community, the microscopic *epilithic* (growing on rock) community. Rocky surfaces are covered by a biofilm comprising microalgae, cyanobacteria, and newly germinated stages of macroalgae. This often slippery biofilm also includes bacteria, protozoans, and meiofauna. In the upper intertidal, cyanobacteria give the rock surface a dark, almost black color. Typical cyanobacterial genera are *Rivularia* and *Calothrix*. However, the black color can also be due to salt-tolerant lichens, such as *Verrucaria maura*. Epilithic diatoms often include life forms that are stalked and form colonies (for example, the genera *Gomphonema, Fragilaria*). The biofilm is an important food source for limpets and periwinkles

and also influences the settlement of invertebrate larvae. In addition to a top–down control by grazers, the algae in the intertidal biofilm are controlled by physical stress caused by high insolation (Thompson et al., 2004).

8.4.3 Coral Reefs

Coral reefs are productive, diverse, and economically important ecosystems that dominate hard-bottomed habitats in low nutrient tropical and subtropical waters. They proliferate in open nearshore habitats and in sheltered lagoons along tropical and subtropical coasts. On pristine coral reefs, fleshy macroalgae are rarely spatially dominant (Littler and Littler, 1984); rather, tropical reefs in low nutrient waters are dominated by crustose coralline and turf-forming algae. These algae form the base of benthic food chains, contribute to biodiversity, and stabilize reef framework. Crustose coralline algae play an important role in reef accretion, cementation, and stabilization (Littler et al., 1995). Algal turfs, comprising filamentous algae and cropped bases of larger forms, are ubiquitous throughout tropical reefs and are characterized by high rates of primary productivity. An exception to dominance by corallines and turfs on pristine reefs can occur when mechanisms exist which limit the efficacy of herbivores. Physical or chemical defenses produced by macroalgae such as *Dictyota* and *Sargassum*, and spatial refuges from herbivory such as surrounding sand planes or the bases of branching corals, can support fleshy macroalgae (Hay, 1984; Smith et al., 2010). Human impacts on reefs such as overfishing of herbivorous fishes (Jackson et al., 2001; Hughes et al., 2003) and increased nutrient supplies (Smith et al., 1981; Lapointe et al., 2005) may also produce dominance by macroalgae.

8.5 SPATIAL PATTERNS OF BIOMASS AND PRODUCTIVITY

8.5.1 Broad Geographic Scale—Latitudinal Differences

Benthic macroalgae are found in subtidal and intertidal estuarine habitats from tropical to polar regions. Some macroalgal species have broad geographic distributions, indicating their ability to acclimate to climatic variations in temperature and irradiance. For example, the foliose *Laminaria saccharina* occurs in rocky subtidal habitats from Spain to North Greenland (Lüning, 1990), and coralline algae inhabit waters throughout tropical and polar regions (Steneck, 1986).

Mesoscale differences in annual rates of productivity are related predictably to temperature and irradiance levels. Rates of productivity can be as high as 2500 g C/m²/year (Valiela, 1995), and highest annual rates are in tropical communities where growth and temperature conditions are favorable throughout the year. In regions where water column productivity is low, as in the tropics and some polar regions, benthic macroalgal production can exceed pelagic production on an areal basis (Duarte and Cebrian, 1996; Krause-Jensen et al., 2007).

Benthic microalgae are found on every surface that is reached by light. While benthic microalgae exist in all climatic zones, their temporal and depth distribution varies with latitudinal light conditions and the transparency of the water column. The range of annual benthic microalgal primary production varies from 5 to over 3000 g C/m²/year, but most values are within the range 20–500 g C/m²/year (Cahoon, 1999), and the highest values are from tropical regions. Areal values of both daily net primary production (NPP) and chlorophyll *a* (a rough measure of microalgal biomass) are often similar in magnitude to those for phytoplankton in shallow, clear water of the coastal regions. In shallow (1–3 m) estuaries, benthic microalgae can account for up to 70% of the total primary production (Underwood and Kromkamp, 1999; Baird et al., 2004), and in areas that lack macroscopic primary producers, they constitute the only autochthonous benthic source of primary production. Even in temperate seagrass meadows, the contribution of benthic microalgae can be 20–25% of the total benthic primary production (Asmus and Asmus, 1985). In tropical and subtropical seagrass-vegetated sediments, the biomass of benthic microalgae can be as high as that in adjacent unvegetated sediments, even though the seagrass canopy reduces light availability at the sediment surface (Miyajima et al., 2001).

8.5.2 Depth Distribution

Benthic macroalgae contain accessory pigments that allow capture of different wavelengths of light and efficient utilization of changing light quantity and quality with depth in the water column (Fig. 8.2). Red algae contain accessory pigments such as phycoerythrin that absorb green and blue-green wavelengths that penetrate deep in clear coastal waters. Crustose coralline red algae are the deepest living marine macroalgae, and have been found at depths of 268 m in the clear, tropical waters of the Bahamas where irradiances were less than 0.001% of the surface irradiance (Lüning and Dring, 1979). These macroalgae are characterized by slow growth rates. Light attenuation with depth, and the changing quality of light

All algae have chlorophyll a (white line in top graph)

The quantity and quality of photosynthetically active radiation (visible light) changes with depth. Blue and green light penetrates deepest.

Green algae also have chlorophyll b and are generally limited to shallow or very clear water

Brown algae have auxiliary pigments such as fucoxanthins that enable them to proliferate at intermediate depths

Red algae can survive at the deepest depths as auxiliary pigments such as phycoerythrin absorb the blue and green light

Although auxiliary pigments enable algae to extend their ranges deeper, this does not mean that they are limited to those depths! Red algae, for example, can live intertidally as well as deep. In addition, other factors such as grazing, wave energy, and disturbance control algal depth zonation.

Artwork by Kendal Fong

FIGURE 8.2 Different divisions of algae have adapted to the varied light regimes that occur along depth gradients in estuaries.

limits the potential depth distribution of macroalgae, although disturbance and grazing losses also influence the actual depth distribution (Fig. 8.2). The minimum light requirements for thick macroalgae (~0.12% of surface irradiance) and thin macroalgae (<0.005%) are substantially less than those for most seagrasses (~10–25%, see Chapter 5), and as a result their depth penetration is much greater than that for the vascular plants (Fig. 8.3).

As for macroalgae, the depth at which benthic microalgal primary production is important depends on the transparency of the water body. In clear waters, benthic microalgal NPP can be substantial at depths >20 m and can be sustained at a light level of $5-10 \, \mu$mol photons/m^2/s (Cahoon, 1999). At a site in NE Greenland, the maximum depth limit for benthic microalgae matched the 50 m depth limit for crustose coralline macroalgae, where light was 0.004% of the

Light

Maximum depth of survival

Maximum light requirements:
Seagrass ~11%, thick macroalgae ~0.12%, thin macroalgae ~0.003%
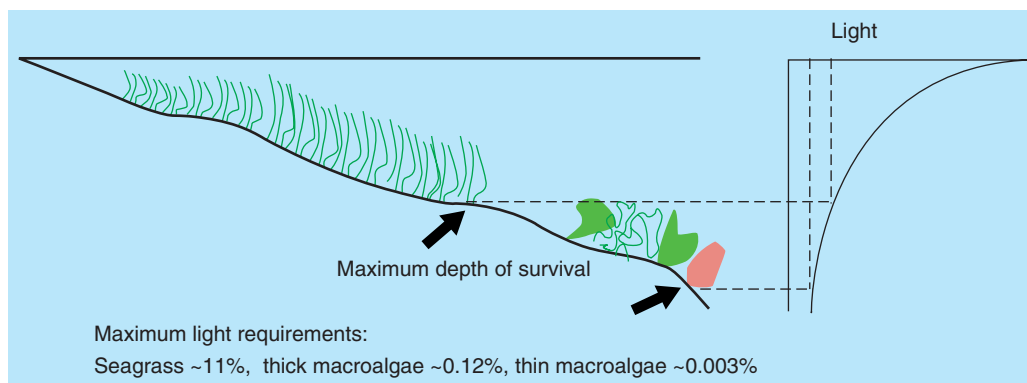
FIGURE 8.3 Comparison of minimum light requirements between macroalgae and seagrass. Depth limits are set by light attenuation in the water column.

surface irradiance during the open-water season (Rysgaard et al., 2001).

8.5.3 Energy Regime

Flow velocities around macroalgal thalli can have positive effects on rates of nutrient uptake and photosynthesis by reducing the thickness of the boundary layer and increasing the exchange of gases and solutes across the thallus surface (Hurd, 2000; Hepburn et al., 2007). In dense macroalgal communities, flow velocity is reduced due to the drag imposed by the thalli and this increases particle deposition and decreases particle resuspension (Gaylord et al., 2007; Morrow and Carpenter, 2008). Reduced flow rates can also influence macroalgal growth. For example, Stewart et al. (2009) showed that in dense beds of the giant kelp *Macrocystis pyrifera*, fronds on the seaward edge of the bed had faster elongation rates, larger blades, and greater carbon and nitrogen accumulation than interior fronds that were exposed to lower flows. Flow velocities also decrease with depth in the subtidal, and maximum velocities typically occur at the subtidal–intertidal fringe (Denny et al., 1985). Biomechanical models for high energy systems (up to 15 m/s) can be used to calculate velocities that cause macroalgal thalli to break and thus predict survival against hydrodynamic forces (Denny, 1995). The two most important factors determining break forces for macroalgae are substrate type and thallus size (Malm et al., 2003). In low energy systems, water speeds as low as 0.22 m/s can cause both breakage and ''pruning'' (thallus fragments left for regrowth) for attached algae with delicate thalli such as *Ulva* (Kennison, 2008). The macroalgal form can vary in response to flow regimes, with exposed areas having algae with flatter, narrower fronds to reduce drag and protected areas having wider, undulate fronds to increase turbulent flow and decrease boundary layer effects. This can reflect both morphological plasticity and genetic differentiation (Hurd et al., 1997; Roberson and Coyer, 2004).

The largest accumulations of macroalgae are found in poorly flushed systems, such as sheltered embayments and estuaries, with elevated nutrient concentrations where bloom-forming species occur (e.g., *Ulva* sp., *Chaetomorpha* sp., *Gracilaria* sp, *Polysiphonia* sp.) (Viaroli et al., 1996; Pihl et al., 1999). Advective transport of macroalgae, both between habitats within an estuary (i.e., subtidal to intertidal) and from the estuary to the coastal ocean, can be important in terms of nutrient exchange. Macroalgal material moves either as bedload or as floating mats at the water surface, depending on their specific gravity (which is influenced by photosynthesis rates and invertebrates that colonize mat-forming macroalgae). Unattached, living macroalgae move at current velocities as low as 2 cm/s (Flindt et al., 2004), and these current velocities are common in estuaries where both winds and tides affect current speeds at the sediment surface (Lawson et al., 2007; Kennison, 2008). Macroalgae also settle 1000 to 5000 times faster than phytoplankton, and hence if transported out of estuaries usually settle on the ocean floor rather than being returned on the flood tide (Flindt et al., 2004). Few studies include mass transport of nutrients bound in plant material and as a result nutrient retention in estuaries can be overestimated.

Generally, benthic microalgal production is higher in fine sediments than in sandy sediments exposed to wave action (Underwood and Kromkamp, 1999). The explanation for this finding is that fine sediments, with high organic matter concentration and rapid bacterial mineralization, contain more nutrients in the pore water than sandy sediments with less accumulation of organic matter. Moreover, the biomass of benthic microalgae (measured as chlorophyll *a* content of the sediment) in the upper few millimeters of muddy sediments can be much higher than in sandy sediments. But the NPP can occasionally be as high, or even higher, in sandy than in muddy sediments. One reason is the higher availability of light, because of a thicker photic zone, so that photosynthesis can occur deeper in sandy sediments than in muddy sediments. In addition, advective flushing can reduce nutrient limitation in inundated permeable sands (Billerbeck et al., 2007). In high energy environments, such as tidal sand flats, a large part of the benthic microalgal community can be resuspended during the tidal cycle, contributing to pelagic production. Up to half of the food resource of filter feeders can consist of resuspended benthic microalgae (de Jonge and Beusekom, 1992). The turnover of benthic microalgal biomass on sandy tidal flats is typically higher than that on muddy flats (Middelburg et al., 2000).

8.6 TEMPORAL PATTERNS OF BIOMASS AND PRODUCTIVITY

8.6.1 Diel Cycle

The diel cycle of benthic microalgal primary production is well described, and generally differs between tidal and subtidal sediments (Fig. 8.4; Miles and Sundbäck, 2000). On muddy tidal flats, there are large variations in the light climate during the day because
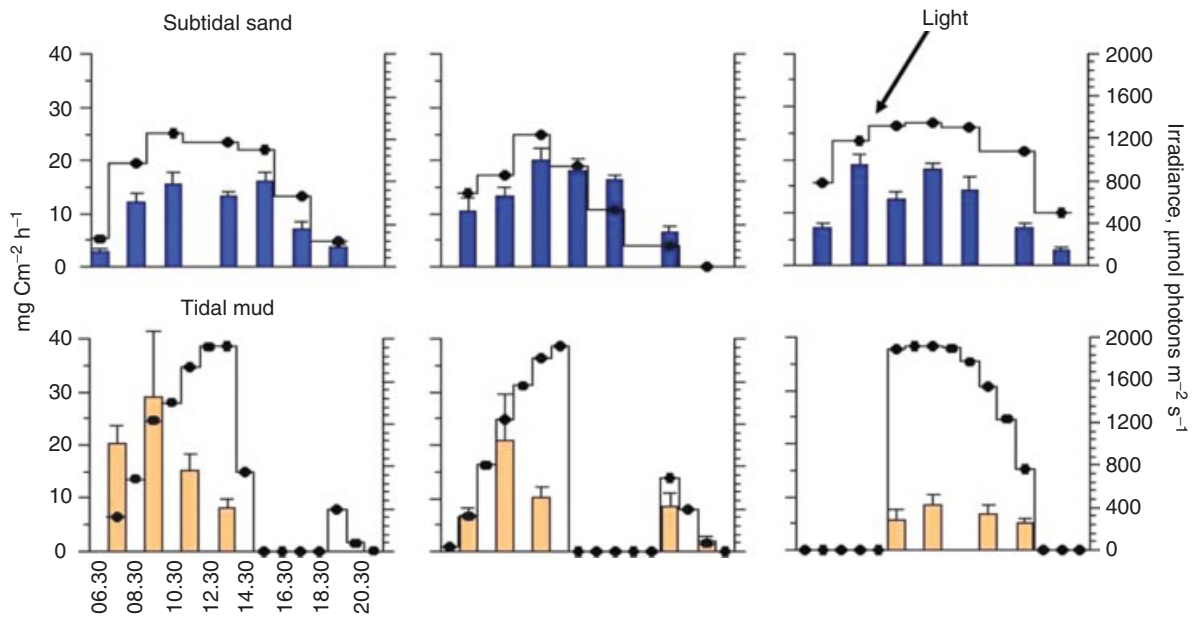
FIGURE 8.4 Diel pattern of microphytobenthic primary production (bars) on a shallow-water subtidal sandy site (Kattegat, microtidal west coast of Sweden) and an intertidal muddy site (Tagus estuary, Portugal). Measurements were made by the ^{14}C technique with subsequent 2-h incubations during three full days. Filled circles show irradiance measured at sediment surface. Because of high turbidity, no light penetrated to the sediment surface during high tide in the Tagus estuary. *Source:* Redrawn from Miles and Sundbäck (2000).

of tide-induced turbidity, and photosynthesis occurs only when the sediment is immersed during daylight. This pattern is strengthened by the endogenous (i.e., controlled by ''internal clocks'') vertical migration rhythm of particularly motile diatoms. The algae start to migrate down 30–60 min before the tide returns (Kromkamp and Forster, 2006) and emerge again to the surface for the low tide period (Fig. 8.1b). High resolution techniques, such as low tempera-ture scanning electron microscopy and single-cell pulse–amplitude–modulation (PAM) chlorophyll fluorescence, have shown that the algal composition at the sediment surface changes during the photope-riod (Underwood et al., 2005). This vertical migration can be explained as a way of taking advantage of the favorable light conditions during low tide and avoiding resuspension by the tidal waves. A more stable habitat with higher concentrations of nutrients also provides more favorable conditions for cell growth and division deeper in the sediment compared to the sediment surface (Saburova and Polikarpov, 2003). On sandy tidal flats, the water column may stay clear during high tide, and primary production can continue when the sediment is submerged. In subtidal habitats and on microtidal coasts, the light climate is often not affected by tidal turbidity, and benthic photosynthesis can proceed throughout the daylight period (Fig. 8.4), showing the highest production at midday. Benthic diatoms also migrate daily in subtidal conditions so that they emerge before sunrise and submerge in the evening (Longphuirt et al., 2006).

8.6.2 Seasonal Cycle

Seasonality in benthic algal growth is highest in polar regions and decreases toward lower latitudes. For perennial macroalgae in polar regions, shade adap-tation is one way of dealing with the dark winter months and the ice cover 10 months of the year. Lam-inarians that dominate these regions have inherently slow growth rates, storage of carbon reserves during the summer period of high productivity, a long life span, and a high resistance to grazing (Lüning, 1990). Macroalgae need to maintain low respiration to min-imize carbon losses during the long winter months, high photosynthetic efficiency at low light when ice still covers the water surface, and the ability to max-imize continuous light in the summer. Laminarians increase their blade surface area to increase light cap-ture and produce new thin blades before the break up of ice cover using stored reserves in old overwin-tering thalli and are poised for rapid growth as soon as the ice-free period begins (Chapman and Lind-ley, 1980; Dunton, 1985). In temperate soft-bottom

systems, macroalgae may be present year-round, and different species have different thermal tolerances and optimum temperatures for photosynthesis, respiration, and growth, so species composition can change with increasing temperature. In general, the respiration rate increases more rapidly with rising temperature than photosynthesis rate, leading to a decrease in the photosynthesis:respiration ratio (P/R).

Ephemeral macroalgae go through boom and bust cycles in many regions, with the mid-growing season population crashing due to high temperatures and self-shading. In some areas such as southern California, floating blooms can occur during any season, with the magnitude and frequency related to land use in watersheds and patterns of nutrient input (Kamer et al., 2001; Boyle et al., 2004). Intertidal macroalgae on rocky shores, especially in higher tidal zones, respond to interactions among monthly and seasonal changes in the tidal amplitude, temperature, and light by changing biomass (Menge and Branch, 2001). Seasonality is much less pronounced in tropical systems, although some exceptions occur. Some coral reef algae show marked seasonal variation in standing stock of carbon (Lirman and Biber, 2000). On Panamanian reefs, algal productivity and biomass accumulation is much higher during the upwelling season (Smith, 2005), suggesting that algal communities are regulated by nutrients in the absence of upwelling.

Seasonal variability in thallus photosynthesis is higher for ephemeral macroalgae than for perennial genera such as *Cladophora* and *Ulva* that grow fast and store little nutrient reserves (Sand-Jensen et al., 2007). Respiration rates typically vary systematically over the year, and increase as temperature and irradiance levels increase. For temperate species, this leads to higher minimum light requirements during summer than winter for photosynthesis to balance respiration. While there are significant changes in the actual production as light and temperatures vary with seasons, the maximum potential production (at saturating light) varies less (Middelboe et al., 2006). This is in part due to changes in species composition and abundance that favor species that have optimal performance at different times of the year.

Long-term studies on seasonality of benthic microalgae are rare. One of the longest seasonal studies (12 years, 14 stations) on benthic microalgal biomass and production is from a tidal flat on the coast of the Netherlands (Cadée and Hegeman, 1977). This study shows that, in temperate areas, the biomass peaks during the warm season. Occasional dips in benthic chlorophyll *a* during summer are explained by strong grazing pressure, particularly by mud snails (such as *Hydrobia ulvae)*. This seasonal pattern agrees with patterns found in shallow subtidal and microtidal areas in temperate estuaries, although well-developed diatom mats have also been found on the sediment surface under sea ice. Such proliferation of benthic diatoms under ice can be explained by the presence of shade-tolerant species, good nutrient availability, and low grazing pressure. In tropical areas, seasonal variations in benthic microalgal abundance can be influenced by the monsoon, such that abundance is lowest during the monsoon and highest during the postmonsoon period (Mitbavkar and Anil, 2006). In polar regions, the length of the productive season for benthic primary production is only about 80–90 days. During this period, the daily microbenthic primary production (172–387 mg $C/m^2/day$) at depths ≤ 20 m has been found to exceed that of phytoplankton (Glud et al., 2002).

8.7 METHODS FOR DETERMINING PRODUCTIVITY

For macroalgae, various methods are used to estimate production, based either on short-term estimates of carbon assimilation/oxygen production or on longer-term growth estimates.

1. ***Growth Measurements*** Frond-marking is a common technique used to estimate growth rates of large, attached macroalgae such as kelps. The fronds, or blades, are marked with holes at the junction between the stipe and the blade where the growth zone is located. The holes are displaced upward as the blade grows and the distance between the hole and the stipe/blade junction represents new growth (Krause-Jensen et al., 2007). This is similar to the leaf-marking technique that is commonly used to measure seagrass growth. Rates of elongation are then converted to production as mass (gram dry weight, gdw) or carbon using conversion rates. For unattached mats or rafts of macroalgae with diffuse growth (growth throughout the thallus), the biomass can be measured directly as wet weight. Algae are collected from a known area of benthos or volume of water, cleaned of mud and fauna, and, if desired and possible, separated into species. Techniques to assure a consistent wet weight are varied, but include blotting the thalli dry or spinning in a salad spinner for a consistent time and rate. The change in the average biomass over time estimates productivity.

2. ***Photosynthesis Measurements*** Measurements of net or gross production as gas (O_2 or CO_2) exchange

provide shorter-term estimates of production, and these can be scaled spatially and temporally based on availability of incident irradiance. Changes in oxygen or dissolved inorganic carbon (DIC) can be measured on individual thalli in light or dark bottles or chambers to estimate the NPP and respiration. Photosynthesis–irradiance ($P–I$) curves can be constructed for each species to derive data on maximum photosynthetic rate (P_{max}), efficiency of light utilization (a), respiration (R), and the saturation and compensation irradiances (I_s and I_c) (Chapter 4). These parameters can be related to light availability at specific water depths using an equation (e.g., $P = P_{max}[1 - \exp(aI/P_{max})] + R$; Platt et al., 1980) and scaled to areal rates of production.

Since macroalgae can grow in dense accumulations, models are used to account for self-shading within the macroalgal communities (Brush and Nixon, 2003; McGlathery et al., 2001). These models scale production in macroalgal mats based on incident irradiance reaching the canopy, known patterns of light attenuation with depth in macroalgal mats, and $P–I$ relationships for individual thalli. This approach is similar to terrestrial canopy models. Sand-Jensen et al. (2007) have modified this approach further to consider variations in thallus light absorbance, canopy structure, and density. The model has been tested for single-species communities of the sheetlike *Ulva lactuca* and the leathery *Fucus serratus* and for mixed-species communities. An interesting result of the model is the stabilizing effect of species richness, whereby multiple species complement each other in absorbing light.

The PAM chlorophyll *a* fluorescence technique is also used to determine relative measures of photosynthetic activity of algal species. These measurements typically provide a snapshot (seconds–minutes) of photosynthetic capacity to acclimate to light conditions. However, they do not easily translate into quantitative measures of photosynthesis in terms of oxygen production or carbon fixation. The PAM technique can be used *in situ* and measures the activity of photosystem II, giving an estimate of the electron transport rate (ETR). Although there is a fairly good linearity between ETR, oxygen production, and ^{14}C incorporation, this relationship can become nonlinear at high irradiances. For a review on this technique see Kromkamp and Forster, (2006).

For benthic microalgae, the best methods for primary production measurements are those that do not disturb the natural physical, chemical, and biological microgradients in the sediment. There are four principal methods that are used for primary production

measurements in sediments. All these techniques have their limitations, and primary production rates determined by the different methods can be slightly different because they measure different aspects of photosynthesis.

1. ***Sediment–Water*** O_2 ***or*** CO_2 ***Exchange*** Oxygen flux is measured as changes in the concentration of oxygen in well-mixed overlying water in benthic chambers or sediment cores. The advantage of this method is that the measurements integrate over a sediment area and that measurements both in the light and dark give three ecologically relevant rates: net primary production (NPP), community respiration (CR), and gross primary production (GPP). Field measurements of benthic primary production on tidal flats during immersion are possible by measuring CO_2 fluxes in benthic chambers (Migné et al., 2004). Disadvantages are that cores and chambers do not replicate natural hydrodynamic and light conditions and may underestimate the flux.

2. ***Uptake of Radioactively Labeled Carbon (***[14]***C-Bicarbonate)*** This is a suitable technique for tracking the fate of carbon in food webs. In sandy sediments, ^{14}C can be percolated a few millimeters into the photic zone of the sediment (Jönsson, 1991). In muddy sediments, percolation does not usually work, and the technique relies on diffusion of the label into the sediments, which results in underestimation of primary production. Slurry incubations disrupt the microgradients in the sediment, but are suitable in experiments where the maximum potential primary production is used as a variable. The stable isotope ^{13}C also can be used for tracking carbon through the food webs (Middelburg et al., 2000).

3. ***Oxygen Microsensors (with a Tip of Only a Few Microns) and Planar Optodes*** These are used for high-resolution nondestructive measurements of oxygen microgradients in the sediment, from which primary production can be calculated by modeling (Fig. 8.5). The dark–light shift microelectrode technique can also be used to measure oxygen production (Revsbech et al., 1981). The classic oxygen microsensor is the oxygen electrode with a guard cathode (Revsbech, 1989), but there are also oxygen optodes that are based on fiber optics (Glud, 2006). The use of microsensors has contributed greatly to our understanding of the temporal and spatial variations among the processes operating in the top few millimeters of the sediment. Planar optodes make it possible to get a two-dimensional picture of the O_2 distribution and dynamics at a given area over many days (Fig. 8.5; Glud, 2006). Such measurements have provided new
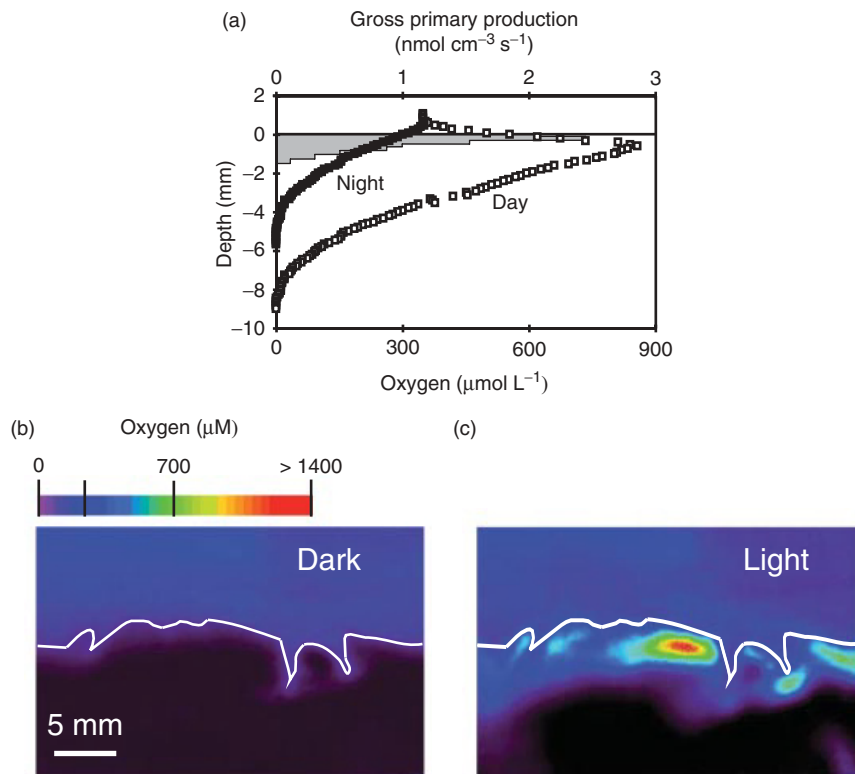
FIGURE 8.5 Influence of microphytobenthos on oxygen distribution in surface sediment. (a) Oxygen profiles in light and dark measured by oxygen microelectrodes. Also shown is a vertical profile of modeled rates of primary production (bars). (b) and (c) Oxygen distribution in light and dark in bioturbated sandy silt measured by planar oxygen optodes (Section 8.7). The bright red spot indicates the high rate of photosynthetic oxygen production in light by an assemblage of benthic diatoms just below the sediment surface. *Source:* (a) Redrawn from Glud et al. (2009) and (b) redrawn from Fenchel and Glud (2000).

insights into oxygen dynamics around rhizospheres, faunal structures, structures in permeable sands, and within phototrophic communities.

4. *PAM Chlorophyll a Fluorescence* The fluorescence technique can be used to estimate photosynthesis in the sediment microalgal community and also to measure photosynthetic activity of individual cells using a modified fluorescence microscope (Underwood et al., 2005)

Finally, for all types of benthic producers, there is a new *in situ* method based on the eddy correlation flux technique that is commonly used to measure oxygen exchange across the land–air interface in terrestrial and intertidal ecosystems. This technique has been adapted to subtidal conditions and has the advantage that it measures community metabolism under natural hydrodynamic and light conditions, can capture short-term (minutes) variation in production/respiration, and integrates over a much larger area (>100 m^2) than conventional techniques (<1 m^2) (Berg et al., 2003, 2007).

8.8 FACTORS REGULATING PRODUCTIVITY AND COMMUNITY COMPOSITION

The mechanisms that control the net production of benthic algae in estuarine ecosystems are the same as those for other primary producers: geographic limits for growth are set by temperature and light. Within the geographical limits, biomass accumulation is controlled by many interacting biotic and abiotic factors including light quantity and quality, nutrient availability, water motion, temperature, intra- and interspecific competition, grazing, and physical disturbance. Here we discuss light, nutrients, and grazing; additional factors are included in other sections.

8.8.1 Light

Similar to all primary producers, benthic macro- and microalgae use visible light in the 400–700 nm

spectrum, which is termed *photosynthetically active radiation* (PAR). Accessory pigments in benthic algae allow certain groups to capture wavelengths that would otherwise be inaccessible by chlorophyll *a* alone (Fig. 8.2). Light is attenuated exponentially with depth in the water column following the Beer–Lambert law, $I_z = I_0 e^{Kdz}$, where I_z is the irradiance at depth z, I_0 is the surface irradiance, and K_{dz} is the attenuation coefficient for diffuse downwelling irradiance. This is described in detail in Chapter 4. The surface irradiance reaching the benthos at a given depth is influenced by properties of the water that affect the attenuation coefficient, including suspended sediment, organic (e.g., phytoplankton) and detrital particles, and colored organic matter (CDOM).

Light is attenuated rapidly within dense macroalgal communities. For the bloom-forming species *Cladophora prolifera* and *Chaeomorpha linum*, 90% of the available irradiance hitting the surface of the mat can be absorbed in the top few centimeters (Krause-Jensen et al., 1996). The extent of this light attenuation will depend on the thallus form (canopy structure) and density of the algae, the absorbance of the algae, and species composition. Complementarity of light use between different algal species in mixed-species communities often means that the total community production is higher for a given irradiance level than for single-species communities (Middelboe and Binzer, 2004). Benthic macroalgae can acclimate rapidly (within minutes) to changing light conditions. This can be an adaptation for optimizing production in a short growing season (Borum et al., 2002) or to a variable light climate due to short-term changes in incident irradiance (e.g., cloud cover) or water column light attenuation (e.g., wind/wave induced sediment resuspension). A general adaptation to reduced light levels is an increase in pigment content and light utilization efficiency. This results in reduced compensation and saturation irradiances (I_c, I_s) for photosynthesis. These characteristics allow macroalgae to more effectively photosynthesize at low light levels. However, the production and maintenance of higher pigment content and enzyme activities increase respiratory costs in low light plants. At high irradiance levels, pigment concentrations are typically lower, compensation and saturation irradiances are higher, and maximum photosynthesis is high. Photoinhibition may occur at high irradiances or under high UV stress, and the damage to the photosystem that causes this inhibition is not necessarily reversible (Chapter 4).

Benthic microalgae also function in a wide range of light climates and are able to adapt to widely fluctuating light conditions. Diatoms can optimize their photosynthetic apparatus efficiently to current light conditions (within minutes) (Glud et al., 2002). Moreover, as epipelic life forms are able to migrate vertically in the sediment, they can position themselves in favorable light conditions. In this way, physiological photoinhibition is avoided at high ambient light levels. Because of back-scattering effects, the light intensity at the sediment surface can be up to 200% higher than the ambient light above the sediment (Kühl et al., 1994). While the photic zone in the water column is generally measured in meters, the photic zone in shallow-water sediments is measured in micro- and millimeters. Fiber-optic microsensors enable high resolution measurements of the light quantity and quality in microbial mats and surface sediments (Kühl et al., 1994). Light penetrates deepest in sandy sediments ($\sim$3 mm), while in fine sediments the photic zone is less than 1 mm. The light climate in the sediment also differs from that in the water column in that red light penetrates deepest in sediments. The vertical change in the light quantity and spectrum often results in stratified microbial mats consisting of layers of organisms with different optimal light requirements (e.g., a sequence of diatoms on the top, followed by cyanobacteria, and then by photosynthetic purple sulphur bacteria, which prefer anaerobic conditions). Live microalgae can be found far below the photic zone in the sediment. Episammic diatoms on sand grains can be mixed down to 10 cm depth in wave-exposed sediments. They survive long periods (weeks, months) of darkness, and rapidly resume photosynthesis when transported up to the photic zone by mixing of the sediment.

8.8.2 Nutrients

8.8.2.1 Sources

Benthic algae obtain nutrients from both the sediments and the water column and the source of nutrients are from both external (allochthonous) and recycled (autochthonous) sources. Sources of ''new'' or allochthonous nutrients include terrestrial inputs via rivers from coastal watersheds, nitrogen fixation, groundwater, atmospheric deposition, and upwelling (Nixon, 1995; Smith et al., 1996; Whitall and Paerl, 2001). With the possible exception of upwelling and N-fixation, all of these sources are rapidly increasing as a result of anthropogenic alterations of global nutrient cycles (for a review, see Vitousek et al., 1997). Autochthonous sources of nutrients include recycling from other biota and regeneration from the sediments during decomposition.

8.8.2.2 Uptake and Storage

The relationship between the nutrient concentration in the water and the rate at which nutrients are taken up by benthic macro- and microalgae can be described by a hyperbolic function. The Michaelis–Menten equation for enzyme uptake kinetics is often used to describe this function, and this is also described in detail for phytoplankton in Chapter 4. The Michaelis–Menten equation describes uptake as follows: $V = V_{max}{}^*[S/(K + S)]$, where V is the uptake rate at a given substrate (nutrient) concentration, S is the substrate concentration, K is the half-saturation concentration—where uptake is equal to $1/2$ of the maximum uptake rate, and V_{max} is the maximum uptake rate at high substrate concentration. From a biological perspective, there are two important components of this relationship: (i) nutrient uptake rates become saturated as nutrient concentration increases and (ii) the initial slope of the curve at low concentrations provides a useful index of an alga's affinity for nutrients at low levels. This latter characteristic may be important in determining the competitive abilities of algae when nutrients are in critically low supply. The V_{max} rate varies depending on the nutrient status of the plant. Algae that have lower nitrogen contents in more nitrogen-limiting environments would be expected to have higher maximum nutrient uptake rates.

For macroalgae, uptake rates are higher for thin-structured sheetlike or filamentous thalli that have a high surface area to volume ratio than for more coarsely branched species (Fig. 8.6, Wallentinus, 1984). In addition, some nitrogen-starved ephemeral macroalgae have the capacity for very rapid (''surge'') uptake during the first minutes of exposure to nutrients, which results in a three-phase pattern of nutrient uptake as a function of external supply (Pedersen, 1994). The capacity for surge uptake is assumed to be advantageous for ephemeral algae subject to short-term nutrient pulses that might result from animal excretion or temporarily high mineralization rates. For macroalgae, there are two primary ways to measure nutrient uptake: (i) the ''multiple flask'' method, where different substrate concentrations are added to individual flasks containing macroalgae, the disappearance of substrate is measured over a short (15-min) incubation, and then the data are pooled to obtain an uptake versus concentration curve; and (ii) the ''perturbation'' method, where thalli are exposed to a high concentration of substrate and a time series of substrate concentration is measured (Pedersen, 1994).

Both macro- and microalgae can store nutrients, and their capacity to do this varies depending on their inherent growth rates and the frequency and magnitude of nutrient pulses. The general pattern that emerges is that fast-growing ephemeral macroalgae such as *Ulva* and *Chaetomorpha* store little reserves compared to slow-growing perennial species such as *Fucus*, which has reserves that can support growth for longer periods of time. This influences the duration
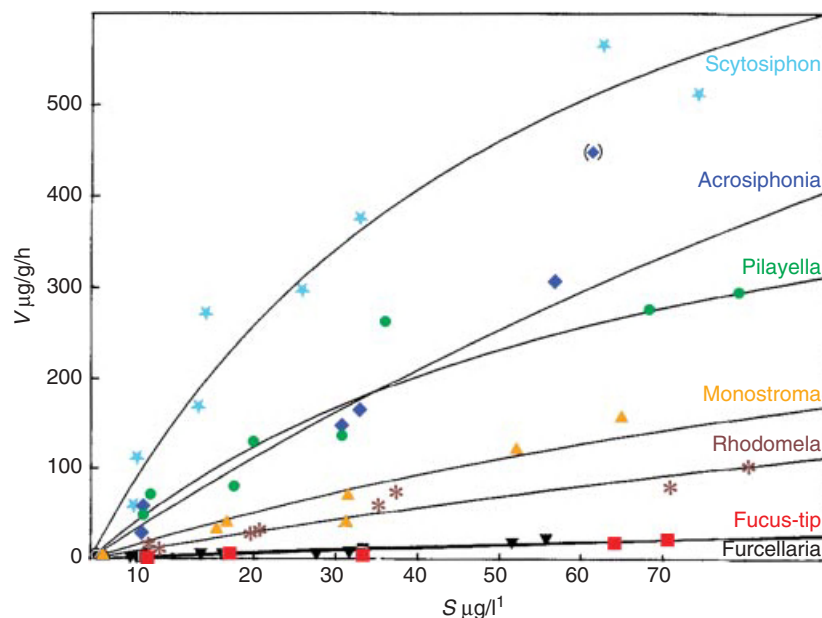
FIGURE 8.6 Maximum uptake rates of NH^4-N versus concentration for macroalgae with different ratios of surface area to volume. *Source:* From Wallentinus (1984).

of nutrient limitation that often occurs in temperate regions in response to a seasonal (summer) depletion of nutrients. For example, Pedersen and Borum (1996) showed that while different algal species, from phytoplankton to slow-growing perennial macroalgae, had similar storage reserves (mg N/gdw), the storage capacity, that is, the ability to support growth in the absence of an external nutrient supply, varied from less than 1 day for phytoplankton to greater than 15 days for perennial macroalgae (Fig. 8.7). On shorter time scales (hours–days), macroalgae have rapid, but transient, responses to variability in N availability, with uptake rates influenced by changing tissue N pools (McGlathery et al., 1996). Also, the coupling of C metabolism (photosynthesis and storage) and N metabolism over the short term implies that algal growth rate acts as a feedback regulator to maintain balanced C-N metabolism, except under extreme conditions of high irradiance and low N supply. Such self-regulation may be especially beneficial

FIGURE 8.7 Periods of nutrient-limited growth (a) and storage capacity (ability to support growth in the absence of an external nutrient supply) (b) for phytoplankton and macroalgae in a Danish Fjord compared to ambient nutrient concentrations. *Source:* From Pedersen and Borum (1996).

to algae growing in estuarine environments that are characterized by high spatial and temporal variability in nutrient and light availability (McGlathery and Pedersen, 1999).

8.8.2.3 Limitation of Growth

In most temperate and polar estuaries, nitrogen is considered to be the primary limiting nutrient for growth, in part due to high rates of denitrification relative to nitrogen fixation. For macroalgae in tropical/subtropical systems dominated by carbonate sediments, phosphorus often limits growth, largely due to the binding of phosphorus by the carbonate sands. There are exceptions to this generalization that are related to the ratio of N:P in external loading, variations in the relative rates of nitrogen fixation and denitrification, and the adsorption capacity of carbonate sediments in different systems. Large data sets on C:N:P ratios of marine plants indicate that macrophytes (macroalgae and seagrasses) have different characteristic atomic ratios of tissue nutrients than phytoplankton. Atkinson and Smith (1983) examined marine plants and found a ratio of 550:30:1 for benthic marine plants, and Duarte (1992) showed that the ratio for 46 macroalgal species was 800:49:1. These ratios compare to the "Redfield Ratio" of phytoplankton of 106:16:1 (Chapter 4), and suggest that macroalgae have a higher nitrogen demand. As with phytoplankton, these ratios are often used to infer nutrient availability and possible nutrient (N vs P) limitation.

Increases in nutrient supplies that relieve nutrient limitation in subtidal soft-sediment habitats result in enhanced macroalgal production and potentially in the loss of seagrasses, which tend to dominate under low nutrient conditions (see Chapter 5 and Duarte, 1995; Valiela et al., 1997; McGlathery et al., 2007). In salt marshes, water column nutrients sequestered by understory macroalgae are retained within the salt marsh community, and become available to support vascular plant growth when macroalgae senesce (Boyer and Fong, 2005). Transitions from macroalgae to toxic cyanobacterial mats occur in estuaries on the West Coast of the United States (Armitage and Fong, 2004), perhaps due to higher tidal amplitudes, lower residence times, and broad areas of intertidal mudflats (large areas of suitable habitat). Nutrient-driven community shifts also occur in rocky intertidal areas (Worm et al., 2002; Worm and Lotze, 2006). In these studies, experimental nutrient enrichment increased macroalgal abundance, and grazing by consumers moderated that response. However, macroalgae in areas with low ambient nutrients responded to enrichment with increased thallus complexity and diversity,
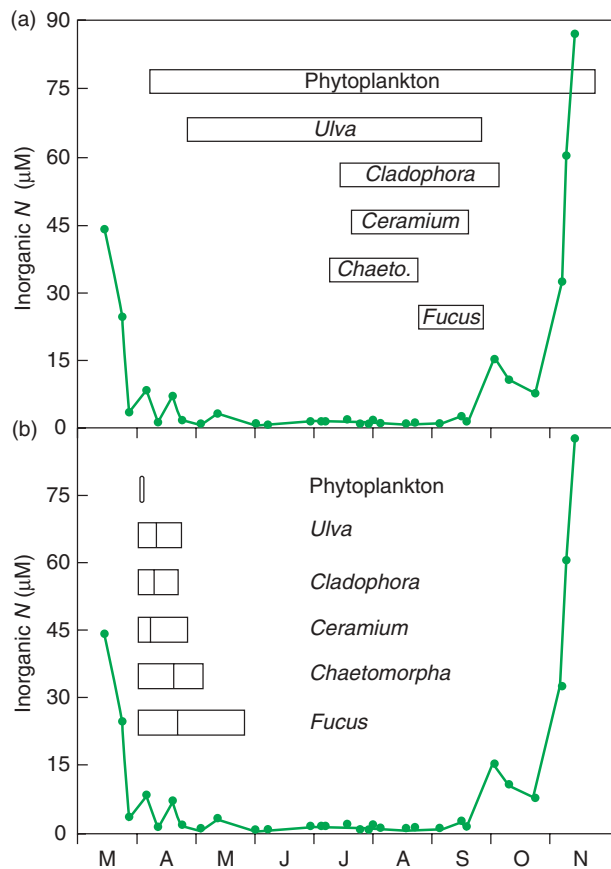
while macroalgae in more enriched areas responded with decreases in diversity due to a shift in dominance to opportunists.

For coral reefs, there is considerable debate about whether algae are limited by nutrients. Effects of experimental nutrient additions have varied from no effects (Delgado et al., 1996; Larkum and Koop, 1997; Koop et al., 2001) to orders of magnitude differences in effects on photosynthesis, growth, and biomass accumulation (Lapointe and O'Connell, 1989). Interpretation of experimental results is limited, in part, by the difficulty of relating results of laboratory or microcosm studies to natural growth in the high energy, high flow environments with variable nutrient supply typical of coral reefs (Fong et al., 2006), and by the related methodological challenge of effectively conducting *in situ* experiments in these same environments (reviewed in McCook, 1999).

It was once generally assumed that benthic microalgae are not likely to be limited by nutrients in the same manner as phototrophic organisms in the water column. This is often the case for fine sediments, but in sandy sediments, benthic microalgae can be nutrient limited (Nilsson et al., 1991). For short periods, however, nutrient limitation can also occur in fine, cohesive sediments during, for example, tidal emersion (Thornton et al., 1999). Studies on nutrient fluxes in well-sorted permeable sandy sediments exposed to wave action have, on the other hand, partly changed our view on the nutrient limitation in sandy sediments. In permeable sediments, nutrient availability can be enhanced by efficient advective transport, resulting in high microbenthic primary production (Billerbeck et al., 2007).

8.8.3 Grazing

Preferential feeding by herbivores can influence the abundance and species composition of macroalgae. Many studies show an association between high nutrient content of primary producers and high consumption rates; however, other factors such as herbivore abundance, per capita grazing rates of the dominant herbivores, and feeding preferences also play important roles in determining patterns of herbivory (Cebrian, 1999, 2002).

Herbivory has been shown to control algal biomass accumulation with community-level effects. For example, grazers such as amphipods and gastropods can control the abundance of algal epiphytes on seagrasses and hard substrates, and can mediate the negative shading effects of epiphytes in response to nutrient loading (Williams and Ruckelshaus, 1993; Hillebrand et al., 2000). Likewise, grazers can mediate the impact of macroalgal blooms in eutrophic environments (Worm et al., 2000). On coral reefs, at low to intermediate nutrient supplies, herbivores can control macroalgal abundance and maintain the competitive dominance of slower-growing community types (Hughes et al., 2003; Pandolfi et al., 2003). Rapid growth with nutrient enrichment allows algae to escape control by herbivores and also biomass to accumulate, which ultimately leads to a phase shift. Chemical and structural defenses also provide a refuge from control by herbivores, allowing algal biomass to accumulate even in heavily grazed areas. In soft-sediment communities, enhanced algal growth from high nutrient loading can saturate the grazing potential and decrease per capita consumption rates; grazer abundance can be impacted negatively by the change in physicochemical conditions (i.e., low oxygen, high sulfide and NH_4^+) that result from the decomposition of algal blooms (Hauxwell et al., 1998).

Microbenthic primary production can enter the food web through several pathways, including through grazers, detritus, or dissolved organic carbon (DOC). Field studies show that a large fraction of benthic microalgal biomass can pass through macrograzers (>1 mm), particularly mud snails (*Hydrobia*) (Asmus and Asmus, 1985; Andresen and Kristensen, 2002). In addition, some microphytobenthic production can pass through the "small food chain" consisting of microfauna (unicellular fauna such as ciliates) and meiofauna (<100 μm) (Fenchel, 1968; Kuipers et al., 1981; Pinckney et al., 2003). Meiofauna have been estimated to occasionally graze up to 100% or more of the benthic microalgal standing stock, although benthic primary production is generally sufficient to supply food resources for meiofaunal grazers (Pinckney et al., 2003).

8.9 ENERGY FLOW

The amount of energy sequestered in primary producers and the proportion flowing through algal-dominated benthic estuarine communities varies among soft sediment, coral reef, and rocky intertidal and subtidal ecosystems (Fig. 8.8). In all systems, the amount of energy that is fixed into algal biomass and made available to higher trophic levels is dependent on resources, usually light and nutrients. Overall, systems more closely associated with terrestrial environments, and those that experience restricted water exchange, such as those composed of soft sediments, are assumed to be subject to and affected the most by increasing external nutrient supplies.
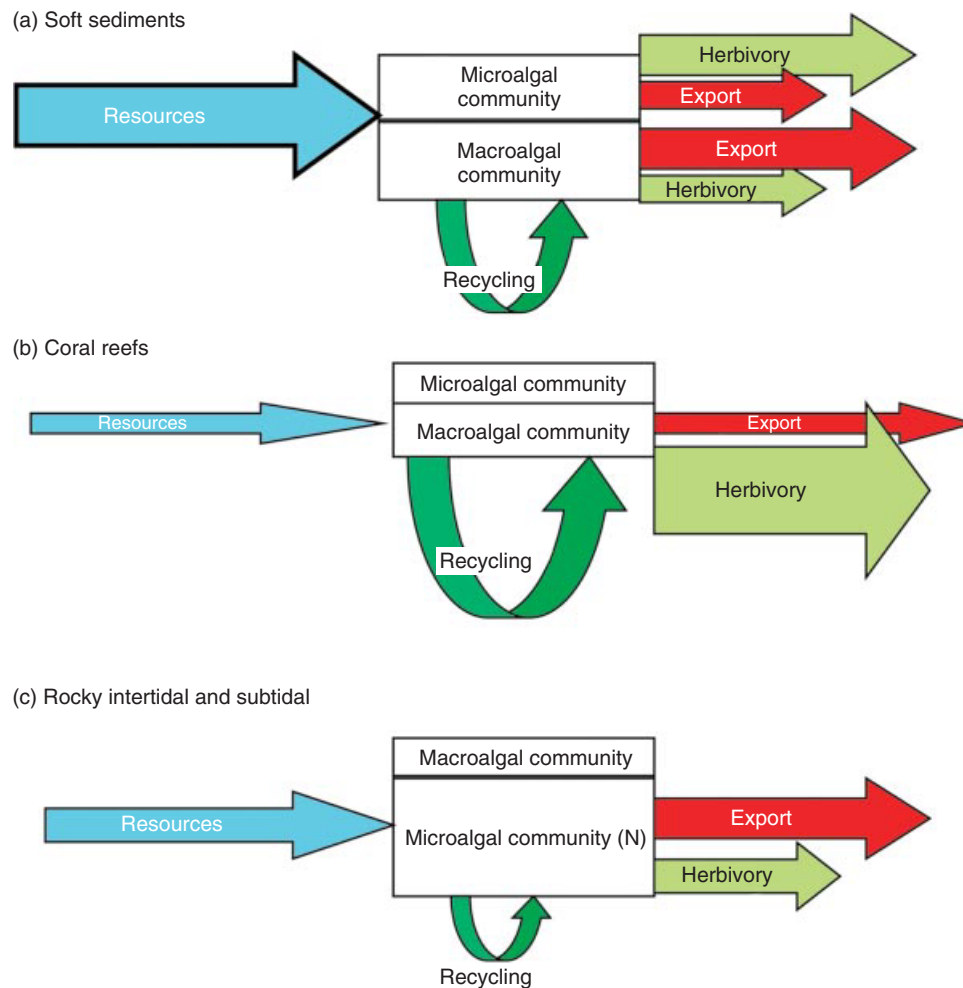
FIGURE 8.8 Energy flow diagrams for different macroalgal communities. The size of the arrow represents the magnitude of flow in the different pathways.

8.9.1 Recycling of Nutrients

Across estuarine systems, recycling of nutrients from sediments and biota is most likely greatest in soft sediment and coral reefs and least in rocky intertidal and subtidal systems. In soft-sediment estuaries and lagoons, fluxes of nutrients regenerated from sediments are an important source of recycled nutrients (McGlathery et al., 1997; Fong and Zedler, 2000; Tyler et al., 2003). In some seasons, fluxes meet up to 100% of macroalgal nutrient demand (Sundbäck et al., 2003). Interception of nutrients by macroalgae may reduce supplies to other producer groups and change the path and rate of carbon flow. Macroalgal communities may also be sustained by nutrient release from senescent or self-shaded thalli, or by recycling of nutrients from nearby vascular plant communities such as seagrass beds (for a review, see McGlathery

et al., 2007). In coral reef ecosystems, recycling from sediments is only likely to be significant in enriched systems (Stimpson and Larned, 2000). Other recycled sources in coral reefs include flocculent material settling on the surfaces of algal thalli (Schaffelke, 1999) and animals that release nitrogenous waste products (Williams and Carpenter, 1988). Release of waste products from closely associated animals is also a recycled source of nutrients in intertidal and subtidal systems (Hurd et al., 1994; Bracken, 2004).

8.9.2 Carbon Storage

The capacity of ecosystems to store energy, represented by the amount of carbon in the biomass of producers and consumers, varies across estuarine ecosystems. An example is the tremendous difference in producer biomass between coral reef algae (0.03–0.6 kg wet weight/m^2 based on a wet:dry

weight ratio of 10:1, Foster, 1987) and rocky subtidal reefs (3.5 kg wet weight/m^2, Manley and Dastoor, 1987). Although both are highly productive in terms of gross primary productivity, they occupy different ends of a spectrum in terms of biomass accumulation and therefore carbon storage. In general, opportunistic species with simple thallus forms such as those that dominate coral reef turfs have low levels of biomass; therefore, they can store little carbon despite having relatively rapid growth rates. The low biomass is due to short life spans, susceptibility to removal and export by physical disturbance, and high rates of grazing by herbivores. In contrast, more complex macroalgae that dominate rocky subtidal and intertidal areas often have high standing stocks of carbon. This is due to the longevity of individual thalli, investment in structure to withstand physical disturbances, and lower rates of carbon transfer to herbivores due to protection by chemical and physical defenses. One exception to this generalization is opportunistic macroalgae in shallow soft-sediment estuaries that go through periods of boom and bust and cycle carbon quickly.

8.9.3 Herbivory

The amount of energy that is transferred from macroalgae through consumption can vary by orders of magnitude across estuary types. On a global scale, direct consumption by grazers was estimated to be 33.6% of the net carbon fixed by macroalgae, demonstrating their general importance as the base of food webs in coastal ecosystems (Duarte and Cebrian, 1996). Herbivory on coral reefs is extremely high, with large herbivorous fishes and invertebrates acting as ''lawn mowers'' that keep algal standing stocks very low and carbon transfer very high (for a review see McCook, 1999; Jackson et al., 2001). In rocky subtidal habitats, grazing is important in maintaining diversity, but cannot always overcome the effects of increased resources (Worm and Lotze, 2006). Within soft-sediment systems, rates of primary consumption can vary greatly (Fong et al., 1997; Giannotti and McGlathery, 2001), and consumption of benthic microalgae can be very important (Asmus and Asmus, 1985; Armitage and Fong, 2004).

Benthic microalgal production forms the basis for the benthic food webs in sediments where macroscopic primary producers are lacking. The main pathway of this fixed carbon into the food web is generally considered to be through macrofaunal and meiofaunal grazers (Duarte and Cebrian, 1996), although the detrital pathway is also important. The microbial film (epilithon) on rocky surfaces is an important component in the cycling of carbon, particularly on exposed and moderately exposed shores with large numbers of limpets and other grazers (Hawkins and Jones, 1992).

8.9.4 Detrital Pathway

Death and subsequent decomposition of macroalgal detritus results in the release and recycling of stored carbon. Processing of carbon through detrital pathways comprises about a third of macroalgal net primary productivity globally (Duarte and Cebrian, 1996). However, like grazing, the relative importance of recycling varies across habitats. For example, high energy rocky areas recycle much less carbon from detritus within the system compared to lagoons, while the estimates for recycling within coral reef algae are very high (Duarte and Cebrian, 1996). When algae decompose, they release organic carbon to the water and, in soft sediments systems, to the sediments (for a review see McGlathery et al., 2007). The detrital pathway is also important for benthic microalgae production (Admiraal, 1984). As much as 70% of the NPP by benthic microalgae on a tidal flat was found to enter the food web as detritus (particulate organic carbon, POC), and was further transferred to bacteria and detritus-feeding fauna (Baird et al., 2004).

8.9.5 Dissolved Organic Carbon

Substantial DOC also ''leaks'' from healthy macroalgal thalli (Tyler et al., 2003; Fong et al., 2003). Some organic compounds in the water can be taken up directly by consumers and may alter food webs toward heterotrophic bacteria pathways (Valiela et al., 1997). A large portion (>50%) of the photosynthetic product of benthic microalgae can also be released as DOC, particularly under low nutrient conditions. This DOC enters food webs rapidly through bacteria (Middelburg et al., 2000), forming the benthic equivalent of the pelagial microbial loop. About 40% to 75% of the carbon fixed by motile benthic diatoms can be released as colloidal organic matter or EPS (Goto et al., 1999; Smith and Underwood, 2000) and rapidly transferred to sediment bacteria.

8.9.6 Export of Carbon

The rate of carbon exported from benthic estuarine communities varies tremendously across ecosystem types and is a function of standing stock, water motion, and algal morphology. Duarte and Cebrian (1996) have calculated that a global average of 43.5% of macroalgal NPP is exported; however, the range is perhaps the more important metric, varying from approximately 0–85% across macroalgal-dominated habitats. Rocky subtidal systems export a far larger

amount of carbon than coral reefs despite vigorous wave action in both systems due to the larger standing stock. In contrast, pristine soft sediment lagoonal systems export less carbon than rocky systems as there is both less physical disturbance and lower water exchange to detach and remove biomass. Thus, seagrasses in lagoons represent a large and relatively stable reservoir of carbon. In contrast, in eutrophic systems there is often accumulation of large floating algal rafts, resulting in faster turnover and more rapid export of carbon to the ocean (Flindt et al., 1997; Salomonsen et al., 1999). In sediments exposed to strong tidal or wave action, benthic microalgae are easily resuspended together with sediment particles and hence can be transported away (Admiraal, 1984). A large study in the Ems-Dollart Estuary (North Sea coast) showed that, on an annual basis, 14–25% of the microphytobenthic carbon was found in the water column as a result of resuspension (de Jonge and Beusekom, 1995).

8.10 FEEDBACKS AND INTERACTIONS

8.10.1 Feedbacks on Biogeochemical Cycling in Soft-Sediment Estuaries

Both macro- and microalgal mats have a large impact on the biogeochemical cycling in shallow-water habitats. This effect can be both direct, through nutrient assimilation, retention, and release, and indirect through oxygen production and consumption, affecting mineralization and other redox-sensitive processes. Despite large differences in biomass, the quantitative role of macroalgal and microalgal mats on biogeochemical processes (for example, nitrogen assimilation) can be similar, making the turnover time of algae-bound nutrients a key factor in nutrient retention in shallow systems (McGlathery et al., 2004). Nutrients that are assimilated by benthic algae are, for the most part, only temporarily retained within individual algal thalli on a time scale of days to months. Tissue turnover times vary for the different autotrophs, with seagrasses having a longer retention time (weeks–months) than bloom-forming macroalgae (days–weeks) and microalgae (days). This suggests that nutrients will be recycled faster in systems dominated by microalgae and ephemeral macroalgae than in those dominated by perennial macrophytes (Duarte, 1995).

Both types of benthic algal mats strongly influence the degree of benthic–pelagic coupling by reducing the flux of remineralized nutrients from the

sediment pore water to the overlying water column (Sundbäck et al., 1991; Fong and Zedler, 2000; Anderson et al., 2003; Tyler et al., 2003; see also Section 8.10.5). Benthic algae can outcompete phytoplankton for nutrients if the major nutrient supply is internal flux from the sediments. Therefore, in shallow coastal systems, short-lived phytoplankton blooms often coincide with low benthic algal biomass (Sfriso et al., 1992; Valiela et al., 1992; McGlathery et al., 2001). The influence of benthic microalgae on sediment–water nutrient fluxes is often observed as lower fluxes—or no flux at all—out of the sediment in light when compared with that in the dark (Sundbäck et al., 1991; Sundbäck and McGlathery, 2005). When sediment nutrient sources are insufficient to meet the growth demand of benthic microalgae, there is a downward flux from the water to the sediment, such that the sediment functions as a temporary *nutrient sink* instead of a nutrient source. This applies particularly to autotrophic sediments (oxygen production exceeds oxygen consumption, Engelsen et al., 2008). Also, dissolved organic nutrients, such as dissolved nitrogen (DON), are influenced by both benthic micro- and macroalgae (Tyler et al., 2003; Veuger and Middelburg, 2007).

Benthic algal mats influence the vertical profiles of oxygen and this affects biogeochemical cycling. The presence of dense macroalgal mats can move the location of the oxic–anoxic interface up from the sediments into the mat since only the upper few centimeters of the mat are in the photic zone where oxygen is produced by photosynthesis (Krause-Jensen et al., 1996; Astill and Lavery, 2001). Below the photic zone, decomposing macroalgae release nutrients that can diffuse upward to support production. Unattached macroalgal mats tend to be patchy and unstable, but oxygen and nutrient gradients develop quickly, in as little as 24 h, suggesting that this filtering function occurs even in dynamic environments (Astill and Lavery, 2001). Overall, sediment nutrient cycling is enhanced by the presence of macroalgae, presumably due to the input of organic matter and faster decomposition (Trimmer et al., 2000; Tyler et al., 2003). In the surface layer of the sediment, dynamic oxygen gradients created by benthic microalgal activity also control the rate and vertical position of the sequence of redox-sensitive processes in the sediment, such as nitrification, denitrification, sulfate, iron and manganese reduction, and methane production.

Benthic micro- and macroalgae have an important influence on rates of denitrification and nitrification. Rates tend to be low in sediments underlying macroalgal mats, likely due to algal competition with bacteria for NH_4^+ and NO_3^-. In addition, high free sulfide

concentrations in organic-rich sediments underlying macroalgal accumulations may inhibit nitrification (Trimmer et al., 2000; Dalsgaard, 2003). In dense macroalgal mats, the zone of denitrification may be moved up from the sediments into the oxic–anoxic interface of the mat (Krause-Jensen et al., 1999). The combined use of oxygen and nitrogen microsensors has shown that benthic microalgae can both reduce and enhance denitrification. During photosynthesis, the oxygenated sediment layer gets deeper, and it takes longer for the NO_3^- to diffuse from the water column to the denitrification zone of the sediment, reducing the rate of denitrification. Under low nitrogen conditions, benthic microalgae will also compete with nitrifying bacteria for NH_4^+, reducing the availability of substrate (NO_3^-) for the denitrifiers. Such an effect by benthic microalgae can still occur down to a water depth of 15 m (Sundbäck et al., 2004). When ambient N concentrations are high, oxygen production will instead stimulate nitrification (an aerobic process), and thereby also stimulate nitrification-coupled denitrification (Risgaard-Petersen, 2003). The alternative pathway of bacterial nitrogen removal, anaerobic ammonium oxidation (anammox), is negatively affected by the presence of active benthic microalgae (Risgaard-Petersen et al., 2004).

8.10.2 Feedbacks on Sediment Stabilization

Macroalgal mats may either stabilize or destabilize sediments, depending on algal abundance. Dense macroalgal mats stabilize sediments by decreasing shear flow at the sediment surface (Escartín and Aubrey, 1995) and thus sediment suspension (Sfriso and Marcomini, 1997; Romano et al., 2003). Thick macroalgal mats (equivalent to 3.5 to 6.2 kg wet wt/m^2) displace velocities vertically and can deflect 90% of the flow over the mat, with only 10% of the flow traveling through the mat (Escartín and Aubrey, 1995). However, macroalgae also exist at low densities and in patchy distributions that are often dependent on available substratum for attachment or on advection of drift algae (Thomsen et al., 2006) and may act to destabilize sediments. At low densities, flow causes macroalgae to move and scour the sediment, increasing sediment suspension relative to bare sediments. This sediment destabilization is akin to the well-documented phenomenon of saltating or abrading particles increasing erosion in cohesive sediments (e.g., Houser and Nickling, 2001; Thompson and Amos, 2002, 2004). In cohesive beds, the critical stress required to initiate erosion is often greater than the stress required to maintain the sediment in suspension. Macroalgae that scrape the bed while moving across it can dislodge particles and increase sediment suspension/erosion.

The influence of benthic microbial mats on surface sediment stability is well studied (e.g., Paterson, 1989; de Brouwer et al., 2006). The mechanism behind this stabilizing effect is the production and extrusion of EPS by diatoms through the raphe during their gliding movements. Its composition can be complex and varies between species, but mainly consists of carbohydrates, proteins, and sulfate groups. EPS bind sediment particles together so that the shear stress needed for erosion of sediment is increased, and therefore the sediment is less easily eroded and resuspended. Besides gluing sediment particles together, EPS also have physiological and ecological implications. On tidal flats, there are large diel changes in environmental variables (light, temperature, salinity, water content, oxygen, and erosive forces). By secreting EPS, the diatoms become embedded in a cohesive matrix that can create more stabile conditions. This sediment stabilization is a seasonal phenomenon at least in temperate systems, and the deposited material may be resuspended at times of the year when the microalgae are less productive (Widdows et al., 2004).

8.10.3 Effects on Faunal Biomass, Diversity, and Abundance

Macroalgae can have positive and negative effects on associated organisms. On the positive side, they can provide a food source through direct assimilation or through detritus-based food chains, as well as a protective refuge from predators (Norkko and Bonsdorff, 1996). The complex structure of some macroalgal species, such as *Gracilaria vermiculophylla*, could potentially create a predation refuge for commercially valuable blue crab and fish recruits as well as shrimps and amphipods in both the subtidal and lower intertidal zones of estuaries (Hay et al., 1990; Thomsen et al., 2009). Macroalgae also may provide an important link between estuarine habitats (subtidal to intertidal, sand flats to seagrass beds), as associated organisms are transferred with advecting macroalgae between habitats (Holmquist, 1994; Thomsen et al., 2009).

The negative effects of dense macroalgae on benthic fauna include harmful exudates that are toxic to some organisms, low dissolved oxygen within and under dense macroalgal mats (Hull, 1987; Isaksson and Pihl, 1992), and high dissolved NH_4^+ concentrations that also can be toxic (Hauxwell et al., 1998). These negative effects have been associated with observed reductions in abundance of various macrofauna, including bivalves, gastropods, amphipods, and fish, as well as increases in certain polychaetes,

oligochaetes, and amphipods (Norkko and Bonsdorff, 1996; Raffaelli, 2000; Wennhage and Pihl, 2007).

Both macro- and microalgal mats can cause negative upward cascades in estuarine food webs. For example, microalgal mats subjected to high nutrient loads shifted to dominance by cyanobacteria and purple sulfur bacteria and increased the mortality of the dominant herbivore, the mudsnail *Cerithidia californica*, threefold over mats subjected to lower nutrients that were dominated by diatoms (Armitage and Fong, 2004). Changes in benthic fauna associated with macroalgal blooms may cause resident and migratory shorebirds to change foraging behavior. For example, sandpipers spend more time probing in their search for food when they are foraging on top of macroalgal mats, but more time repeatedly pecking when mats are absent (Green, 2010). As infauna are a major food source for birds and other secondary consumers, macroalgal impacts that reduce this link in the food chain may impair this vital ecosystem function. There is also growing evidence that indirect positive effects in the form of ''facilitation'' cascades mediated by habitat created or modified by macroalgal species can enhance biodiversity and organismal abundancs (Thomsen et al., 2010).

8.10.4 Facilitation by Fauna

Macroalgae in soft-bottom environments can be facilitated by fauna, such as tube-dwelling polycheates and bivalves, that provide hard substrate for settlement and growth. For example, the tube-cap forming polychaete, *Diopatra cuprea*, facilitates macroalgal assemblages in shallow lagoons. These organisms create and maintain attachment sites by incorporating algal fragments into tube caps, thus increasing algal residence time on mudflats compared to unattached algae (Thomsen et al., 2005). This association both increases population stability and resilience by providing a stable substrate that retains algae against hydrodynamic forces such as tidal flushing and storm surge, and by providing new fragments to populate new areas or repopulate areas after a storm disturbance. Oyster reefs and mussel and clam beds likewise provide substrate for algal attachment and increase both biomass and diversity relative to nearby bare sediments (McCormick-Ray, 2005). These biotic substrates also enhance algal growth by local fertilization effects. Grazers such as the California Horn Snail can facilitate the development of macroalgal mats by consuming microalgal competitors and releasing nutrients for uptake by macroalgae (Fong et al., 1997). Also, on coral reefs, Carpenter and Williams (1993) showed that urchin grazing facilitated algal turf production by reducing self-shading within the dense algal turf community. Invertebrate grazers that remove microalgal

films that sometimes form on macroalgal thalli, but do not damage the macroalgae, may facilitate macroalgal growth by enhancing nutrient and gas exchange.

8.10.5 Competition between Benthic Algal Primary Producers

Competition between benthic and pelagic algae was mentioned briefly in Section 8.10.1. Here we discuss the interplay between mats of benthic microalgae and loose mats of opportunistic macroalgae in shallow water in more detail (Fig. 8.9).

Benthic micro- and macroalgae interact, directly and indirectly, through their impact on light, oxygen, and nutrient conditions. The type and strength of the interactions change with the growth phase, physiological state, the spatial location of the mats in relation to each other, and the type of the water body as it relates to tidal amplitude. Shading by dense macroalgal mats generally decreases benthic microalgal production. However, shade-adapted microphytobenthic communities that remain active—and even thrive—below macroalgal mats are also present, provided that at least some light penetrates to the sediment surface (Sundbäck and McGlathery, 2005). An example of such a shade-adapted species is the large sigmoid diatom *Gyrosigma balticum*. Benthic microalgae, particularly diatoms, are in fact often resistant to short-term (days, few weeks) hypoxia and anoxia and promote recovery of sediment systems by rapidly reoxygenating the sediment surface after hypoxic and anoxic events (Larson and Sundbäck, 2008).

When nutrient concentrations in the water column are low, primary producer groups compete for nutrients. In such a situation, the importance of sediments as a source of remineralized nutrients increases. At the same time, an active benthic microalgal mat will decrease the availability of sediment nutrients, limiting the growth of loose macroalgal mats, as well as phytoplankton. In Figure 8.9, two conceptual models are shown: one where the macroalgal mat (MA) exists close to the sediment surface (Fig. 8.9 a, b) and the other where the macroalgal mat is floating at the water surface (Fig. 8.9 c, d). The coupling also depends on the thickness of the macroalgal mat and the time of the day (day/night, tidal cycle).

8.11 ENVIRONMENTAL IMPACTS

8.11.1 Eutrophication

As estuarine systems become increasingly eutrophied and macroalgal blooms occur, the decomposing macroalgal mats contribute significant amounts of organic matter to the water and sediments (Trimmer
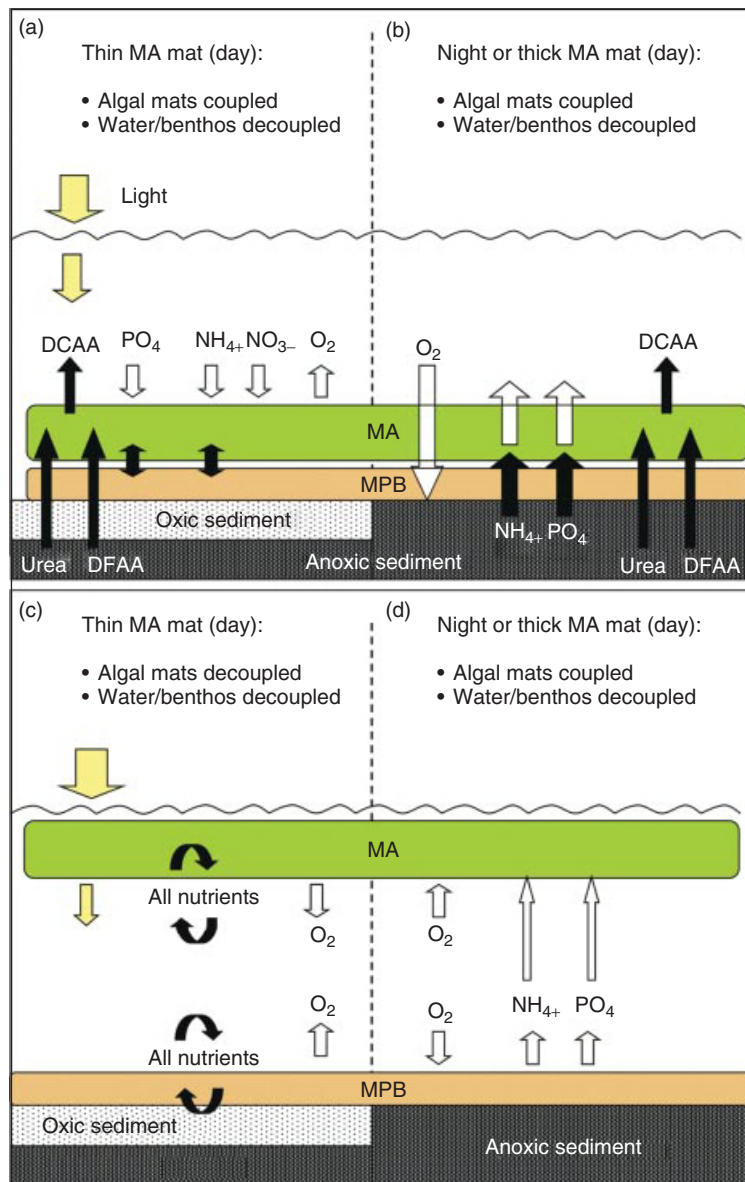
FIGURE 8.9 Conceptual models of interactions between mats of benthic microalgae (microphytobenthos, MPB) and loose macroalgae (MA). Upper panel (a and b): macroalgal mat lying close to the sediment surface, a situation common on tidal coasts during low tide. Lower panel (c and d): macroalgal mat floating at the water surface, a typical situation in microtidal waters. In (a), the two closely coupled mats intercept nutrient release from the sediment to the overlying water, whereas in case (b) nutrients are released from the anoxic sediment and the coupled mats to the overlying water. When the two algal mats are spatially separated (c and d), there is no nutrient exchange between the two mats or between the sediment and water column. Instead, algal productivity is sustained by efficient recycling of nutrients within the mats themselves (c). This scenario applies particularly to autotrophic (often sandy) sediments in microtidal areas when nutrient levels in the overlying water column are low. At night, or when a thick floating macroalgal mat does not allow light to penetrate to the sediment surface (d), pore-water nutrients are released to the water column where they can be used by floating macroalgae. DFAA refers to dissolved free amino acids, and DCAA refers to dissolved combined amino acids. *Source:* Model drawings were inspired by the model in Astill and Lavery (2001) and redrawn from Sundbäck and McGlathery (2005).

et al., 2000; Tyler et al., 2003; Nielsen et al., 2004). This decomposing organic matter turns over relatively quickly and is a positive feedback mechanism that increases nutrient availability to sustain large algal standing stocks. Other consequences of algal bloom formation in eutrophic estuaries include decreases in fish/invertebrate abundance and diversity, anoxia, and loss of seagrasses, corals,

and perennial algae (see 8.10). Eutrophication can lead to phase shifts from seagrass communities to algal-dominated communities (Hauxwell et al., 2001; Valentine and Duffy, 2006), similar to what has been observed in lakes and several other ecosystems (Scheffer et al., 2001; Scheffer and van Nes, 2004). It is essential to know whether these transitions are reversible phase shifts or if they represent an alternative state stabilized by negative feedbacks (Fig. 8.10).

Tropical estuaries with coral reefs may also undergo phase shifts from coral to algal domination (Knowlton, 2004), although the link to eutrophication is less well established than for soft-sediment habitats. One classic study in Kaneohe Bay (Hawaii, USA) established that hard-bottomed communities shifted from coral to algae and back to coral again with changes in nutrient loading. In this system, sewage outfalls into the Bay increased nutrients and stimulated phytoplankton blooms. Lower light penetration stressed corals, shifting the competitive advantage to the macroalga *Dictyospheria cavernosa*, the ''green bubble algae'' that was able to creep over the substrate and replace coral. After sewage was diverted to an offshore outfall, water clarity increased and coral gradually recolonized and replaced the algae. However, while Kaneohe Bay is a clear example of a eutrophication-driven transition from coral- to algal-dominated tropical reef communities, several other studies suggest that co-occurring stressors, such as the loss of grazers, must be in play to shift these communities (Pandolfi et al., 2003).

The growth of benthic microalgae also may respond to increased nutrient load, particularly in sandy sediments with lower concentrations of pore-water nutrients than finer sediments (Nilsson et al., 1991). It appears that microphytobenthic communities are highly resilient to eutrophication-related disturbances and may play an important role in the resilience of the sediment community after, for example, hypoxic and anoxic events (McGlathery et al., 2007; Larson and Sundbäck, 2008). The negative impact of eutrophication on the benthic microalgal community may be more gradual and slower than for benthic macroscopic primary producers such as seagrasses. Thus, a partial beneficial ''buffering'' effect of benthic microalgae on shallow sediment systems may persist even in more heavily eutrophied systems. Microphytobenthic communities possess, owing to high diversity and functional redundancy, a certain degree of plasticity, increasing the overall resilience of shallow-water sediment systems after pelagic bloom events. Benthic diatoms can survive periods of only a few % of incident light (or even darkness), and high sulfide levels, and can rapidly resume photosynthesis when exposed to light or after an anoxic event (Larson and Sundbäck, 2008 and references therein). This scenario, with benthic microalgae surviving despite deteriorating conditions, may apply particularly to areas where macroalgal bloom events last only a few months (Pihl et al., 1999; McGlathery et al., 2001; Dalsgaard, 2003), leaving the rest of the year open to benthic microalgal primary production. In warm, eutrophic microtidal systems with long-lasting macroalgal blooms, benthic microalgae can be outcompeted by shading and also by dystrophic events when the macroalgal blooms eventually collapse (Viaroli et al., 1996).

8.11.2 Invasions

A recent review by Williams and Smith (2007) identified a total of 277 introduced macroalgal species in marine waters worldwide. The primary vectors for invasion are boat traffic and aquaculture. Most reports are from temperate regions; there is a general lack of information on introduced species from tropical waters, especially coral reef habitats (Coles and Eldredge, 2002). The taxonomic distribution of invasive species identified in the review included 165 Rhodophytes, 66 Phaeophytes, 45 Chlorophytes, and 1 Charophyte. Most successful invaders were foliose and filamentous forms, followed by leathery and siphonous forms (Williams and Smith, 2007).

Several characteristics of successful invaders have been identified: rapid reproduction and the potential for successful evolution in new habitats, rapid colonization (including fragmentation as a source of new propagules), vegetative growth for population stability, rapid nutrient uptake and growth potentials (''weedy'' species), antiherbivore defenses, and a wide environmental tolerance (Nyberg and Wallentinus, 2005). Both physical disturbance (by killing natives and opening space) and eutrophication (by relaxing resource competition) can make estuarine habitats more easily invaded. Some well-known invasions are those of *Caulerpa taxifolia*, *Gracilaria vermiculophylla*, *G. salicornia*, *Kappaphycus alvarezii*, *Hypnea musciformis*, *Sargassum muticum*, and *Codium fragile* (Fig. 8.11). In general, the community-level effects of invasive macroalgae are negative when accumulations are dense, and include shading of native algal species leading to decreases in abundance and diversity, decline in epifaunal and fish abundance, diversity and reproduction, loss of seagrass, and increases in incidences of anoxia and

The Nature of Community Collapse: Phase Shifts or Alternative Stable States?

Macroalgae are taking over benthic estuarine communities worldwide. Catastrophiccollapses from long-lived seagrass and coral dominated ecosystems to opportunistic and shorter-lived macroalgae have focused research on the nature of these shifts. One important question is whether these are simple and reversible phase shifts, or if they represent alternative stable stateswith stabilizing mechanisms that inhibit recovery to the initial state (Scheffer et al. 2001, Beisner et al. 2003, Didham and Watts 2005).

Phase shifts

Alternative stable states - shifts along an environmental gradient

Phase shifts are rapid, catastrophic shifts from one dominant community to another over a very short range of environmental change. Incremental changes in a environmental conditions cause little change until a critical threshold is reached. Thus, the past history of environmental change will not aid prediction of future change.

Communities that exist as **alternative stable states** also undergo rapid and catastrophic changes. However, forward transitions occur at different points than backward transitions resulting in a range of conditions (between F1 and F2) where either of two different states can occur. Thus, there is limited ability to predict the community state based on the condition of the environment.

Why do we care?

Management strategies differ if communities exist as alternative stable states. Theory predicts there are only two ways to restore the initial, often more desirable state.

One is to reverse the environmental conditions far beyond the forward shift, to F_2, often a very difficult and expensive option.

The other is to cause a large disturbance that pushes the community beyond the unstable equilibrium (represented by the dotted lines), a strategy with unknown side effects.

To distinguish phase shifts from alternative stable states scientists must search for positive feedback mechanisms that stabilize each state that are strong enough to buffer these states across a range of environmental conditions (betweenF_1 and F_2) and provide resilience to small disturbances.

Alternative stable states - shifts in response to disturbance

Small disturbances return tooriginal state

Large disturbances (past unstable equilibrium) shift toalternate state

FIGURE 8.10   The Nature of Community Collapse: Phase Shifts or Alternative Stable States?

hypoxia. There may be cases where introduced seaweeds increase habitat structure and complexity on unvegetated mudflats, as is the case with *G. vermiculophylla* in some Virginia coastal lagoons, and have a positive effect on faunal abundances as long as algal populations stay below bloom proportions (Thomsen et al., 2009).

8.11.3 Climate Change

Climate change impacts on benthic algae include sea-level rise, increased temperature, increased CO_2 in the air and water, ocean acidification, and changes in weather patterns (Parmesan and Yohe, 2003). Rising temperatures have been predicted to cause poleward shifts in geographic ranges of species and ultimately alter the composition of marine communities (for a review see Hawkins et al., 2008), including benthic primary producers in estuaries. In temperate latitudes, warming may result in deepening thermoclines and relaxation of cold upwelling, thus enabling warm water species to more easily jump gaps in distribution, especially along the western margins of major continents. Continued temperature increases in tropical systems will likely result in further increases in dominance of benthic algae as a result of coral bleaching and mortality (Hoegh-Guldberg, 1999). Changes in storm frequency may influence the distribution and abundance of benthic primary producers in estuaries by reducing or enhancing intertidal and shallow subtidal habitat via sedimentation, reducing water clarity and the depth of the photic zone, and increasing scouring (Zedler and West, 2008). For example, experimentally simulated scouring by sediments shifted the algal community from a diverse assemblage of macroalgae to more opportunistic forms (Vaselli et al., 2008) with high temporal variability (Bertocci et al., 2005) in rocky coastal habitats.

Some experimental evidence as well as studies of aquaculture optimization techniques suggests
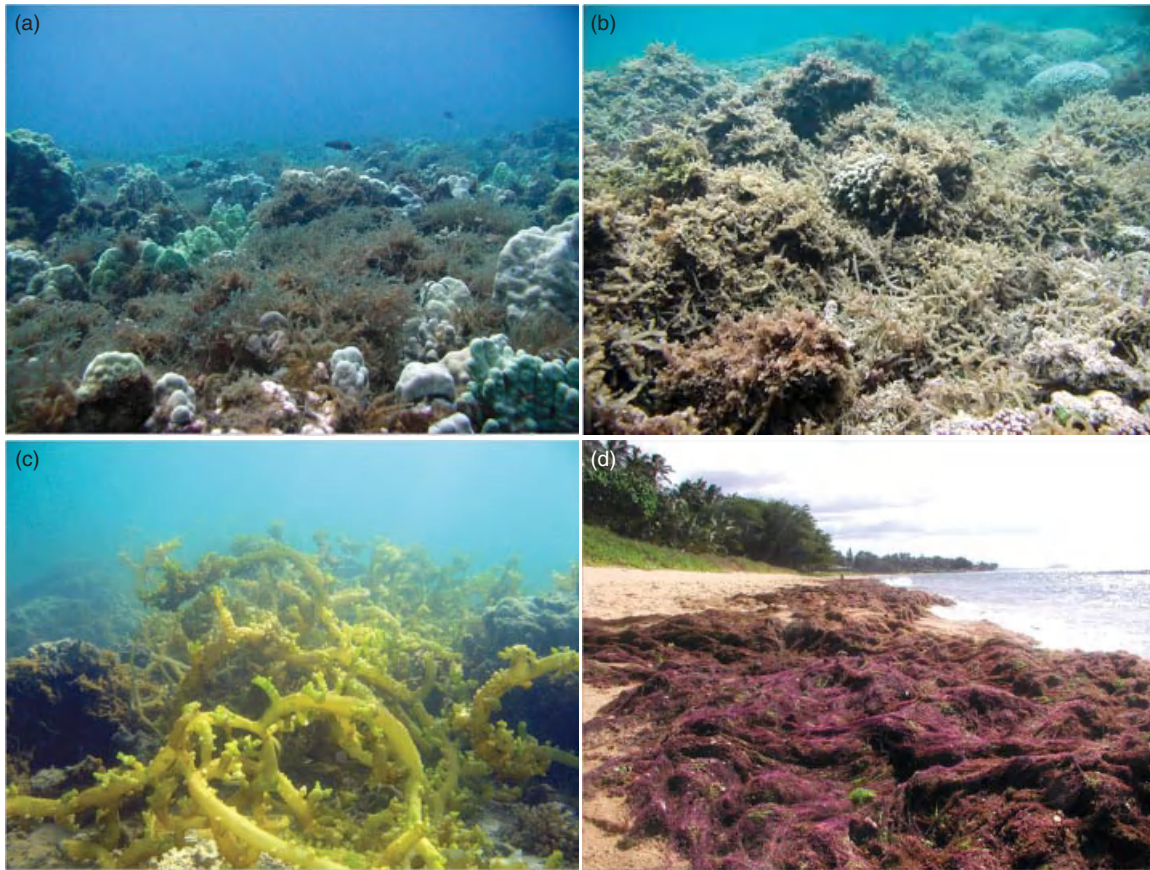
FIGURE 8.11 Many species of invasive red algae proliferate on Hawaiian coral reefs including (a) *Acanthophora spicifera* (b) *Gracilaria salicornia*, and (c) *Kappaphycus alvarezii*. (d) In some areas, such as the coast of Maui, blooms of *Hypnea musciformis* become so large that they detach, form floating rafts, and deposit on the beach. *Source:* Photographs by Jennifer Smith.

that increased CO_2 concentrations and the resultant acidification of seawater may have strong effects on estuarine algae. Experiments with elevated CO_2 and lowered pH have revealed strong negative effects on tropical crustose calcareous algae (Jokiel et al., 2008; Anthony et al., 2008), and also show that *Porphyra* growth decreased with increased CO_2, most likely due to increases in dark respiration rates (Israel et al., 1999).

There is also evidence that complex interactions among factors may be important. For example, while increased temperature and nutrients may increase algal recruitment and growth up to some threshold, they should also increase the number of grazers, driving intertidal communities toward opportunistic species and away from dominance by fucoids (Lotze and Worm, 2002). O'Connor (2009) found that warming strengthens herbivore–algal interactions, shifting important trophic pathways. Recent multifactorial experiments show that certain stages in complex life cycles may be more sensitive to interactions among

climate-related factors and may be important bottlenecks limiting the ability of algal dominants to survive climate change over the long term. For example, while adult kelp sporophytes in polar regions are relatively hardy to changes in temperature, UV light, salinity and their interactions, germination of zoospores is much more sensitive (Fredersdorf et al., 2009). Aquaculture studies have identified an important interaction between rising CO_2 and nutrients, with positive CO_2 effects on growth of *Gracilaria* being accelerated with pulsed nutrient supplies (Friedlander and Levy, 1995), suggesting that storms combined with rising CO_2 will facilitate algal blooms in estuaries. Other studies suggest that interactions among climate change factors may result in changes in habitats. In sheltered embayments of the North Sea, rising sea level and eutrophication combined to cause shifts from *Zostera* to opportunistic green macroalgae (Reise et al., 2008). Overall, it appears that interacting factors associated with climate change will enhance algal blooms, and may shift communities to greater algal dominance.

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CHAPTER NINE

ESTUARINE MICROBIAL ECOLOGY

Linda K. Blum and Aaron L. Mills

9.1 INTRODUCTION

Microbes are critical in controlling the function and structure of estuarine ecosystems through activities that include nutrient cycling, organic matter decomposition, and conversion of indigestible detrital materials to form more ''palatable'' to large consumers. This chapter addresses what microbes are, where microbes are found in estuaries, and what microbes do in estuaries with a focus on bacteria, fungi, and viruses. This chapter provides an overview of how microbes metabolize organic and inorganic compounds to obtain energy and building blocks for biosynthesis, and how these processes influence nutrient cycling in estuaries. The role of microbes in food web dynamics is the topic of Chapter 10. Heterotrophic protists (i.e., single-celled eukaryotes) are also discussed in Chapter 10 because of their contribution to ecosystem respiration, and their importance in the transfer of bacterial carbon and energy to higher trophic levels. Microalgae (i.e., phototrophic protists) are discussed in Chapter 4 because of their importance to estuarine primary production.

9.2 BRIEF SURVEY OF MICROSCOPIC ORGANISMS

Microbes are very small, but they are also very abundant. This may seem like a trivial statement, but the reality is that the distribution of many critical processes carried out in ecosystems, including estuaries, is determined by the distribution of tremendous numbers of these tiny individuals of many different types. A single milliliter of estuarine water typically contains around a million individual bacterial cells, although the numbers may be substantially higher in cases where the organic content of the water is enriched above average. There are a number of advantages to being small. The accumulation of nutrients and elimination of wastes are diffusive processes that are more rapid when the cells' surface-to-volume ratio is large. In other words, the interaction between the cell and the environment is facilitated by the microbe's small size. Under conditions favorable to growth, abundance of the active cells can increase rapidly, altering the structure of the microbial community and the relationship between the various groups of microorganisms. While the environment often exerts control over the rates of microbial growth and metabolism (chemical reactions that occur within the cell), the environment also is altered by the activities of the huge number of microbes, even though individual microbial cells are very small. The ability of the microbes to alter the environment is a consequence of their great abundance and rapid growth and metabolism.

Even though microbes are small—a microscope is generally required to see individuals—they exhibit a wide diversity of sizes and forms. Estuaries host all five general groups of microbes: bacteria, algae, protozoa, fungi, and viruses. Viruses are unique in

that they are acellular; they are usually considered to be nonliving entities because their reproductive capacity and energy acquisition is integrally linked to host organisms. The remaining groups fall into three domains proposed by Woese and Fox (1977), and references therein, the Archaea, Bacteria, and Eukarya (Fig. 9.1). The Archaea and Bacteria are prokaryotic: they do not have a nucleus surrounded by a membrane, and they have distinctly different cellular structure compared with the nucleated or eukaryotic protists, fungi, algae, plants, and animals. The cyanobacteria (historically referred to as *blue-green algae*) are members of the Bacteria, along with most cultured bacteria, and all known disease-causing (pathogenic) bacteria (note the use of the common parlance in which the uncapitalized word bacteria refers generally to all the prokaryotes and Bacteria refers to the specific phylogenetic domain). Each of the microbial groups exhibits a variety of morphologies, a range of sizes, and different cell architectures (Fig. 9.2).

9.2.1 Bacteria and Archaea

Bacteria (i.e., Bacteria and Archaea) constitute an extremely abundant and diverse group of microorganisms. They exhibit a wide range of metabolic properties, yet relatively simple morphology (sphere, rod, spiral, and filamentous forms). They usually range in size from <0.2 to 15 μm, although some are much larger, such as the colorless sulfur-oxidizing bacterium, *Thiomargarita namibiensis*, which has a diameter of 750 μm (Schulz et al., 1999). Although

exchange of genetic material between cells is not uncommon, reproduction is by asexual binary fission. Genetically, the Archaea and Bacteria may be as distantly related as the Bacteria and Eukarya (Williams, 1996). The unifying feature of the Bacteria and Archaea is their prokaryotic cell structure.

Bacteria are abundant in all estuarine habitats (Table 9.1). Sediments and salt marsh soils generally harbor more bacteria per unit volume than the water column (10^7–10^{10} cells/cm^3 for typical sediments vs 10^5–10^7 cells/cm^3 in most estuarine waters). Bacterial densities (and growth rates) in the estuarine water column generally are higher than in nearby coastal marine or river waters (Fig. 9.3) and tend to be highest in surface waters and associated with turbid regions.

The Bacteria are highly abundant in estuaries and are responsible for a wide range of activities from organic matter decomposition to elemental transformations of nitrogen, sulfur, and iron. The Archaea make up a small but significant fraction of prokaryotic abundance in estuarine water columns (Bouvier and del Giorgio, 2002; Garneau et al., 2008) and sediments (Munson et al., 1997; Abreu et al., 2001). Estuarine Archaea examined in culture include halophiles, methanogens, and ammonia oxidizers. Some other marine and coastal Archaea are heterotrophic (Kirchman et al., 2007), some fix nitrogen (Burns et al., 2002), and some are chemoautotrophic and capable of CO_2 fixation (Herndl et al., 2005). Characteristics of the organisms examined to date suggest that the
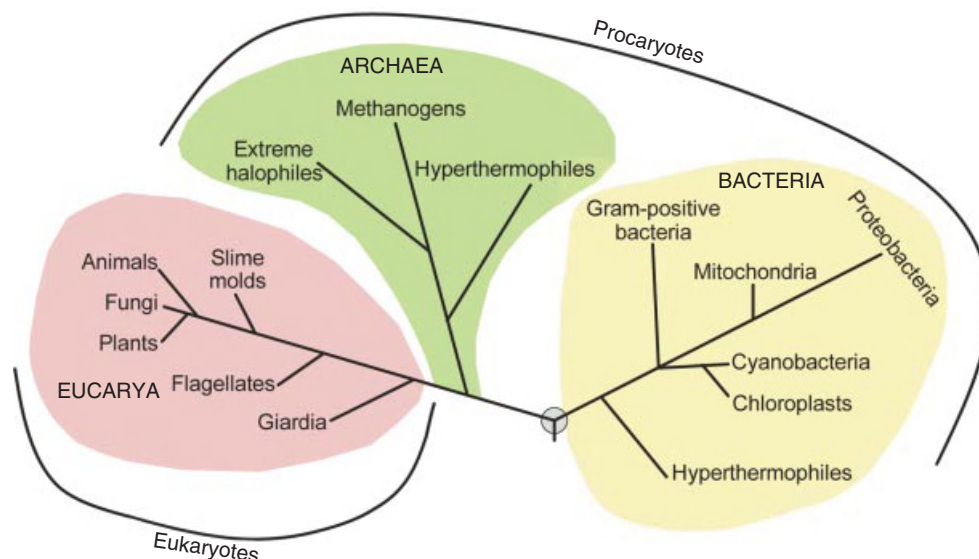
FIGURE 9.1 The three domains of life based on phylogeny as determined by similarity in the genes coding for the small subunit of the ribosome. *Source:* Based on Woese et al. (1990).

Representative sizes and morphologies

Procaryotes

Bacteria

5 µm

Cyanobacteria

25 µm

Eucaryotes

Protozoans

50 µm

Fungi

250 µm

Noncellular

Viruses

0.25 µm
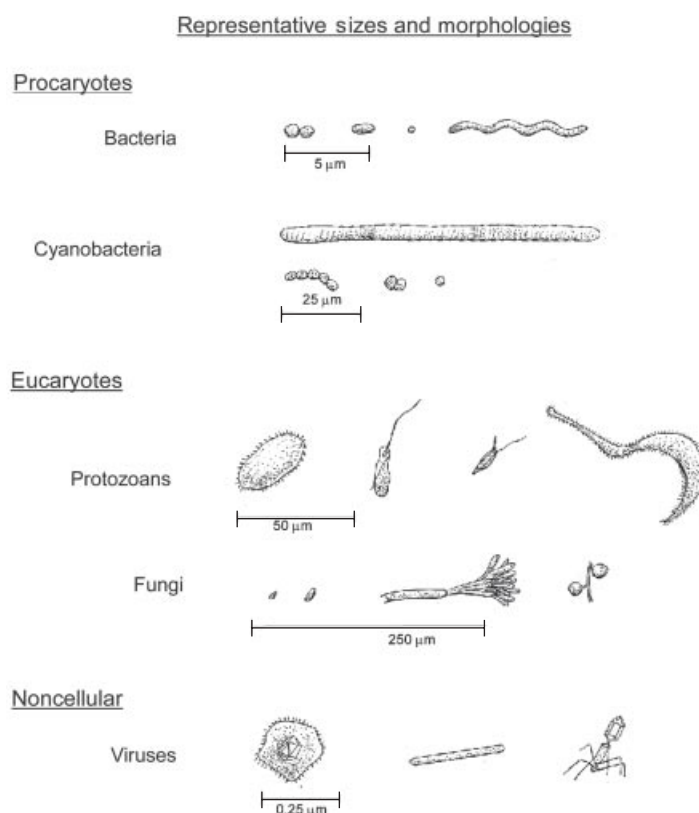
FIGURE 9.2 Comparison of representative morphologies, sizes, and architectures of microbes found in the estuarine environment. *Source:* Figure redrawn from Day and Christian (1989).
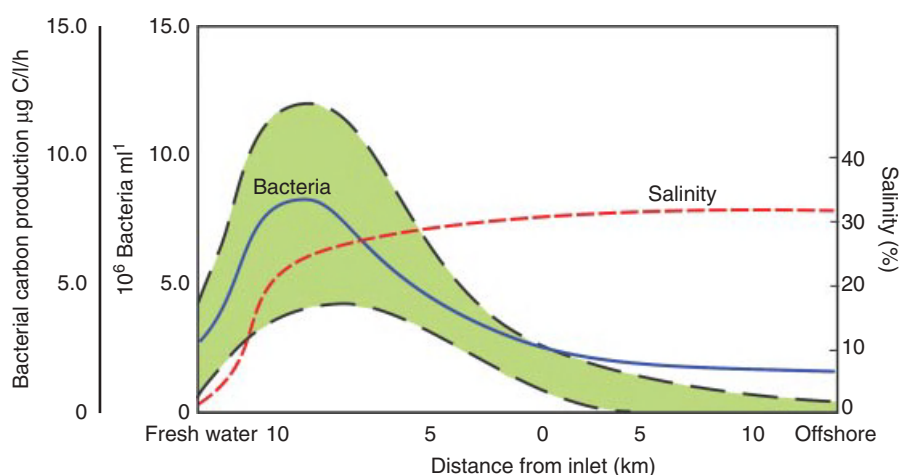
FIGURE 9.3 Longitudinal distribution of bacterial density and productivity in the Essex estuary (northern Massachusetts) and connecting offshore waters. The temperature range was 15–20°C. The gray area between the dashed lines represents the range of observed values for bacterial production. *Source:* Figure redrawn from Wright and Coffin (1983).

Archaea participate in many of the same ecosystem processes as the Bacteria. Indeed, while many new organisms have been discovered, many fewer new processes have been found, such that in the future, rather than finding many new processes that are carried out by the Archaea and Bacteria, continued emphasis on prokaryote diversity will yield a more complete and accurate understanding of which of the new organisms contribute to the processes that we already observe.

TABLE 9.1 Abundance of bacteria in several estuarine and coastal marine locations as determined by direct epifluorescence microscopic counts

Habitat	Location	Density of cells	Reference
Water	Sapelo Island, GA	10^6–10^7/ml	Wiebe and Pomeroy (1972)
Water	Kaneohe Bay, HI	$\geq 10^3$/ ml	Wiebe and Pomeroy (1972)
Water	Continental Shelf, GA	10^3–10^5/ml	Wiebe and Pomeroy (1972)
Water	Kiel Fjord, Germany	1.6–5.7×10^6/ml	Meyer-Reil (1977)
Water	Kiel Fjord, Germany	0.8–2.7×10^6/ml	Meyer-Reil (1977)
Water	Newport R. Estuary, NC	1.95–18.4×10^6/ml	Palumbo and Ferguson (1978)
Water	Humber Estuary, UK	4.6×10^5–5.6×10^6/ml (attached), 4.6×10^4–3.0×10^5/ml (free)	Goulder (1976)
Water	Three estuaries and coastal waters, Massachusetts, United States	0.7–7.0×10^6/ml	Wright and Coffin (1983)
Surface layer of water	Palo Alto Salt Marsh, CA	2.5×10^7/ml	Harvey and Young (1980)
Subsurface water	Palo Alto Salt Marsh, CA	5.4×10^6/ml	Harvey and Young (1980)
Spartina raft interstitial water	Sapelo Island, GA	2×10^7/ml	Wiebe and Pomeroy (1972)
Sediment	Sapelo Island, GA	10^6–10^7/ml	Wiebe and Pomeroy (1972)
Sediment	Petpaswick Inlet, Canada	1.2×10^8–1×10^{10}/g dry wt	Dale (1974)
Salt marsh soil	Newport R. Estuary, NC	8.4–10.9×10^9/cm^3 (surface), 2.2–2.6×10^9/cm^3 (20 cm)	Rublee and Dornseif (1978)

9.2.2 Fungi

Fungi are eukaryotic, heterotrophic microorganisms that form filaments (hyphae), although some are unicellular (e.g., yeasts) for all or part of their life cycle (Fig. 9.4). Many of the fungi exhibit complex life cycles and morphology. Both sexual and asexual reproduction may occur within the same species. Fungal abundance in soils, sediments, and the water column is not reported in this chapter because the studies reporting fungal abundance are based on cultivation techniques (Bayliss-Elliott, 1930; Pugh, 1961, 1962; Pugh and Beeftink, 1980) that do not accurately reflect the true abundance. Techniques that accurately measure fungal biomass have not been applied to estuarine systems because it is commonly accepted that fungal activity is limited in anaerobic sediments and are, therefore, unimportant (Padgett et al., 1986), even though it is clear that hyphae may grow in reducing environments (Padgett et al., 1986; Padgett and Celio, 1990; Mansfield and Barlocher, 1993; Hackney et al., 2000).

What can be said with certainty is that a large number of fungal species and fungus-like protists (e.g., thraustochytrids and labyrinthulids) can be
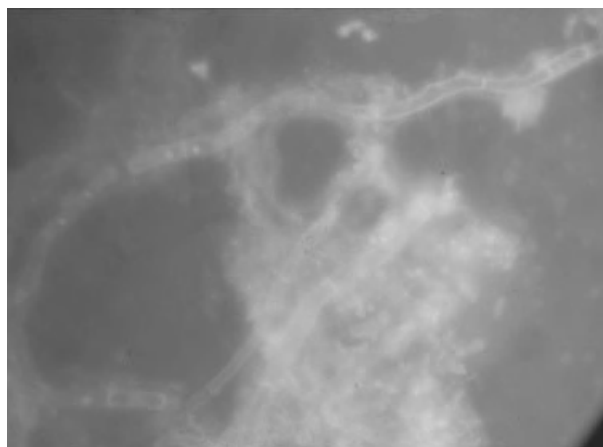
FIGURE 9.4 Image of decaying detritus showing fungal hyphae.

found in estuarine systems (Johnson and Sparrow, 1961; Kohlmeyer and Volkmann-Kohlmeyer, 1991), but what are their activities is still a question that has not been answered with certainty except for a few cases. For example, over 100 species of higher filamentous fungi are associated with standing-dead

plants of salt marsh grasses in the genus *Spartina* (Kohlmeyer and Volkmann-Kohlmeyer, 2002). Fungi may compose 50% or more of the dry mass of those plants (Newell et al., 1989), are largely responsible for their decomposition (Newell et al., 1985), and may also serve as a food source for snails that are commonly found on the plants (Newell and Barlocher, 1993).

Mycorrhizae are mutualistic relationships (beneficial, but not obligate) between fungi and the roots of vascular plants that confer a competitive advantage to the plant and promote rapid establishment of plants after a disturbance. The competitive advantage enjoyed by mycorrhizal plants makes this association of interest to restoration practitioners. Estuarine mycorrhizal plants include the marsh grasses, *Spartina patens*, *Juncus roemerianus*, *Spartina cynosuroides*, and *Distichlis spicata* (Cooke et al., 1993; Hoefnagels et al., 1993; Cooke and Lefor, 1998; Hildebrandt et al., 2001; Burke et al., 2002; Bauer et al., 2003; McHugh and Dighton, 2004), and mangroves (Lee and Baker, 1973; Kothamasi et al., 2006).

9.2.3 Viruses

Viruses are infectious agents that have a genome containing either DNA or RNA and can alternate between two distinct states, intracellular and extracellular (Madigan and Martinko, 2006). They are metabolically inert and rely on a living cell (host) to carry out the metabolic functions necessary for virus replication. Virus particles, or virions, carry viral nucleic acid from one cell to another. Viruses are exceptionally diverse and probably infect all organisms in estuaries, including animals, fungi, plants, and bacteria. Most contain RNA. A few viruses contain single- or double-stranded DNA, but never both RNA and DNA. Viruses also vary widely in size and shape.

Viruses are abundant in estuaries (Fig. 9.5), ranging from 10^4 to over 10^9 virus-like particles (VLPs) per milliliter of water (summarized in Wommack and Colwell, 2000) and from 10^7 to over 10^9 VLP/cm^3 of sediment (Drake et al., 1998; Hewson et al., 2001; Table 9.2). Bacteriophage (often referred to as *phage*), or viruses infecting bacteria, constitute the majority of virioplankton in estuaries (Wommack and Colwell, 2000). The virus-to-bacteria ratio in the estuarine water column is usually much >1 (Cochran and Paul, 1998; Drake et al., 1998) and can exceed 85 in nutrient-rich, highly productive waters (Hewson et al., 2001). Although virus particles are typically 10 times (or more) smaller than bacterial cells, it is the interaction of the individual bacterium and virion that is biologically important, so that the ratio of individuals is the appropriate comparison in this case (Table 9.2).

Beyond differences in abundance, VLPs exhibit high morphological and genetic variability, both spatially and temporally, and it is the highly dynamic nature of the virioplankton that suggests an active role for viruses in microbial communities (Fuhrman, 1999; Wommack and Colwell, 2000). Viruses function to affect microbial community structure as agents of disease and as agents of heredity depending on

TABLE 9.2 Abundance of virioplankton, as virus-like particles (VLPs), in estuarine environments

Aquatic environment	Method	10^6 VLP/ml	Virus/bacteria	Depth, m	Season	References
Lake Saelenvannet, Norway	TEM	20–300	50 ± 30	1 and 2	Spring	Tuomi et al. (1997)
Tampa Bay	TEM	6.3–24.3	—	0	Spring–Fall	Jiang and Paul (1995)
Tampa Bay	TEM	27–46	—	0	Summer	Boehme et al. (1993)
Tampa Bay	TEM	6–34	—	0–10		Paul et al. (1991)
Tampa Bay	TEM	4.8–20	0.9–9	0	Year	Jiang and Paul (1994)
Tampa Bay	TEM	5.2–16	0.4–9.3	0	Year	Cochran and Paul (1998)
Cyanobacterial mat, Texas	ELM	960	—	0	Winter	Hennes and Suttle (1995)
Chesapeake Bay	TEM	2.6–140	3–26	0–30	Year	Wommack et al. (1992, 1995)
Chesapeake Bay	TEM	10.1	3.2	1	Spring	Bergh et al. (1989)
Gulf of Bothnia, Sweden	TEM	17.5–50	11.6	25–230	Spring	Cochlan et al. (1993)
Mid-Atlantic coastal lagoon	ELM	3–9	1.1–2.5	0	Fall	Blum (unpublished data)

Methods include transmission electron microscopy (TEM) and epifluorescence light microscopy (ELM).
Source: Data from Table 1 in Wommack and Colwell (2000).
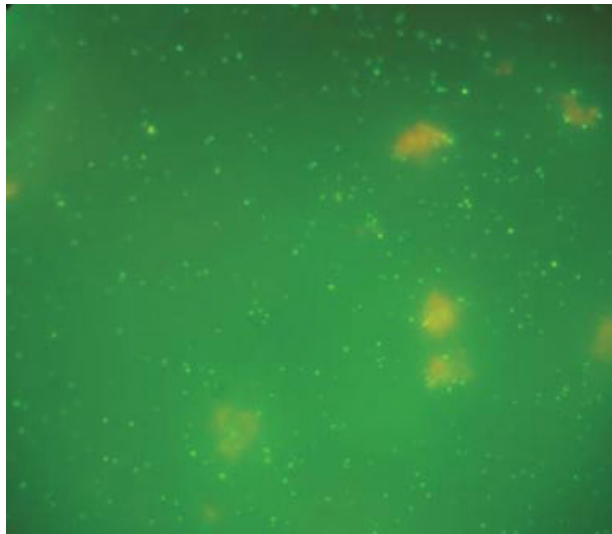
FIGURE 9.5 Epifluorescence microscope field at 1000′ that contains virus particles stained with Syber Green II (Invitrogen Corp.). The particles were trapped on a 0.02-μm pore-size filter after the sample was passed through a 0.2-μm filter to remove bacteria and larger particles.

the type of host cell, the host cell's physiological condition, and the local environmental conditions (Madigan and Martinko, 2006). In either case, viruses may influence estuarine biogeochemical processes and food webs through their effect on community structure (comprising composition, phylotype richness, and evenness—relative phylotype abundance) and individual genomes (function).

9.3 APPROACHES FOR OBSERVING AND MEASURING MICROBES

It is far beyond the scope of this chapter to provide a comprehensive description of the methods available to microbial ecologist. For information about specific methods, *The Manual of Environmental Microbiology* (Hurst et al., 2006) is an excellent resource. Other useful resources include *Aquatic Microbial Ecology* (Kemp et al., 1993), *Aquatic Microbiology* (Ford, 1993), *Methods for General and Molecular Microbiology* (Reddy et al., 2007), *Bergey's Manual of Systematic Bacteriology* (Boone and Castenholz, 2001), and the collected works of Kohlmeyer and colleagues (Kohlmeyer and Volkmann-Kohlmeyer, 1991–2002). Our objective is to provide an overview of some general approaches that are used in estuarine studies, and more specific

examples of principles and applications may be found in Table 9.3.

Questions of interest to estuarine ecologists about microbial communities generally are (i) how big is the community? (ii) are two (or more) communities different? and, most frequently, (iii) what is the community doing? Thus, the study on estuarine microorganisms most often involves quantification and identification of the microorganisms present in a habitat, as well as measuring their activity.

Direct identification of all the microorganisms in water, sediment, or plant litter is not currently possible because the microbes are so small, so abundant, and so many cannot be distinguished morphologically. Identification by any means is also complicated by the diversity of different types of organisms, multiple life stages, and genetic plasticity exhibited, especially by prokaryotes. Often, a whole community approach is taken to study microorganisms in estuaries. In such an effort, the community is studied as a unit rather than examining the individuals composing that unit. Regardless of the question being asked about the community, each of the approaches to answering these questions provides a different view of the community and each has limitations that must be considered in interpretation of the data. Often the question of interest requires that multiple approaches be used to assess the community.

Three general approaches to study microorganisms in natural environments are available to microbial ecologists: (i) direct microscopic observation of the microorganisms, (ii) examination of the results of growth of the microorganisms in some type of culture medium, and (iii) detection and analysis of molecules such as membrane components, enzymes, genes, and gene products extracted from environmental samples or experimental treatments. Methods relying on growth of organisms are called *culture-dependent methods*. Culture-independent methods rely on direct microscopy and observation or detection of molecules (e.g., phospholipid fatty acids, cell membrane proteins, and cell wall components) and genes and other nucleic acids. The activities of microorganisms in their natural environment (i.e., *in situ*) are measured using a wide variety of chemical and biochemical techniques to detect changes in the amount of intermediate metabolites or metabolic end products.

9.3.1 Microscopy

Direct, microscopic observation of microbial communities is the oldest method of obtaining information about microorganisms. This approach has the advantage of revealing the physical relationship among

TABLE 9.3 Approaches for observing microbial community structure

Approach	Type of information obtained	Reference
Microscopy	Abundance of cells, live cells, broad groups, and in combination with molecular approaches, specific taxa	Lawrence et al., 2007
Culturing	Abundance of viable, culturable organisms; physiological studies	Wolfaardt et al., 2007; Garland et al., 2007
Immunological	Quantification of specific groups but requires a pure culture of target organism to prepare antibodies	Campbell, 1993
Lipids	Relative abundance of specific groups containing signature lipid(s); can indicate cell stress	Hedrick et al., 2007; Findlay and Dobbs, 1993
Low molecular weight RNA (5S rRNA/tRNA)	Community similarity	Hofle and Brettar, 1996
Nonsequence-based DNA	Community similarity by homology; number of genomes in community by reassociation	Torsvik et al., 1990
16S rRNA and 23S rRNA	Identification of individual taxa without culturing (TRFLP, DGGE)	Pace et al., 1986; Olsen et al., 1986; Ward et al., 1990
Fragment-based fingerprinting	Community similarity (RAPD, AFLP, TRFLP, DGGE, ARISA)	Franklin et al., 1999; Franklin et al., 2001; Avaniss-Aghajani et al., 1994; Muyzer and Smalla, 1998; Brown et al., 2005
Quantitative polymerase chain reaction	Relative abundance of taxa (QPCR)	Giovannoni et al., 1990
Fluorescence *in situ* hybridization (FISH)	Combined with microscopy or flow cytometry allows quantification of the proportion of individuals within particular taxonomic groups	Wallner et al., 1995
Metagenomics	Community similarity; ultimately identity of each individual within community; currently only practical in exceptionally small communities	Reviewed in DeLong, 2005; NRC, 2007
Metatranscriptomics	Ultimately, functional capability of each individual	Frias-Lopez et al., 2008; Gilbert et al., 2008; Shi et al., 2009

Abbreviation: QPCR, quantitative polymerase chain reaction.
Source: After information in the study by Kemp et al. (1993) and Fuhrman (2007).

cells and between the cell and its environment. At the same time, direct observation provides a way to measure total cell abundance and biovolume of community members but reveals little about their identity or activity. By the end of the 1980s, typical abundances of prokaryotic cells were established for estuarine habitats using microscopic techniques (Table 9.3). By combining biochemical approaches (including those based on genes) with direct observation, the abundance of live cells, functional groups, specific populations (i.e., genotypes), or specific enzymatic reactions can, in some cases, be quantified.

9.3.2 Culturing

Culture-based methods are important because they allow for detailed study on the metabolic processes of an organism or community under carefully controlled conditions in the laboratory. Classically, culture-based methods were applied to enumerate the portion of the community capable of growth under the conditions imposed on the culture. However, work with culture-independent methods has shown that the organisms recovered by cultures are often not the most abundant in any specific environment, and therefore may not be the most important in carrying out ecosystem functions of interest. Nevertheless, such approaches have provided valuable information about the environmental conditions conducive to critical biogeochemical processes and some of the genes and enzymes involved in a specific step in a metabolic process. The tremendous metabolic diversity of microbes, especially the bacteria, in most environments limits the utility of culture-based methods for estimation of abundance and identity of the community because

the conditions necessary to grow one type or group of organism(s) can limit the growth of other kinds of organisms. Thus, in culture-based examinations of environmental samples, usually only a tiny fraction of the total community can be grown in a single medium; furthermore, there are a large number of organisms that have yet to be grown in any culture, pure or mixed. These limitations have prompted most investigators to turn to culture-independent methods, which yield a fraction of the community that is more representative of the whole community of microbes.

9.3.3 Molecular and Molecular-Genetic Approaches

Culture-independent molecular and molecular-genetic approaches are commonly used to examine structural differences in microbial communities (Table 9.3). Immunological approaches have been used to quantify the abundance of specific groups of microorganisms (e.g., nitrifiers, sulfur oxidizers, and cyanobacteria). Analysis of lipids can be used to characterize community structure based on lipids that are unique to microbes and that vary systematically among different microbial groups. An ever-increasing suite of molecular-genetic techniques are employed for analysis of specific types of microorganisms and of microbial communities. Since their application to environmental samples beginning in the early 1980s, many new, previously uncultivated microbes have been observed, and in some cases, classified and named, and the tremendous diversity of microbes in estuaries has been recognized. These culture-independent techniques are commonly used to assess the compositional differences in microbial communities.

All culture-independent techniques can yield information about community similarity based on shared marker molecules or nucleic acid sequences. Fingerprints of communities can be generated and used to test hypotheses about community similarity in both space and time through proper numerical analysis of the data (usually involving multivariate ordination techniques), even though the data may or may not contain information that can be used to identify the organisms (e.g., Franklin et al., 1999; Wikstrom et al., 1999; Franklin and Mills, 2006; Winget and Wommack, 2008). When the question of interest is, ''Are two communities different and how different are they?,'' lipid-based, nonsequence-based DNA, 16S rRNA sequence-based, and fragment-based approaches, as well as other several other approaches not discussed here, are appropriate. If the question of interest requires information about the identity of specific taxa, then approaches that rely on extraction and amplification of small-subunit (SSU) ribosomal RNA genes (16S rRNA for Bacteria and Archaea or 18S rRNA for Eucarya) are used. The SSU rRNA genes are used because they contain highly conserved regions (i.e., they change slowly over evolutionary time) interspersed among more variable regions, making SSU rRNA particularly useful for phylogenetic (evolutionary-based) classification of individuals (Woese et al., 1990; Theron and Cloete, 2000).

Several emerging approaches offer great potential for moving understanding of estuarine microbial community far beyond what we currently know. For example, a variety of fluorescent *in situ* hybridization (FISH) approaches use fluorescent dyes that attach to known SSU rRNA sequences. Depending on the specificity of the fluorescent probe, the types of cells that can be quantified can be broad (Bacteria or Archaea) or as narrow as individual phylotypes. By combining microautoradiography, a traditional approach to determine whether a cell is carrying out a specific process, with FISH, it is possible to determine whether a specific cell type carries out a specific process (Cottrell and Kirchman, 2000; Teira et al., 2004). In the future, the use of laser confocal microscopy in combination with FISH will allow examination of the spatial relationship between specific phylotypes within a microbial community (Lawrence et al., 2007).

Advancements in high throughput DNA sequencing technology, such as 454-pyrosequencing, have made the metagenomics approach feasible for community structure analyses that are not possible with SSU rRNA-based, phylogenetic approaches. The aim of metagenomics is to sequence and identify all the genes from an entire community and, in some cases, to assemble the genes into entire genomes for each individual type of organism within the community such that information about community structure in a classic ecological sense (i.e., both phylotype richness and evenness) is obtained. At the time this was written, there were a few metagenomic surveys in estuarine environments (Cottrell et al., 2005; Bench et al., 2007; Hardeman and Sjoling, 2007). However, in the near future, inexpensive next-generation gene sequencing techniques will allow further exploration of microbial community structure in estuaries. As metagenomic approaches become more widely used it may become possible to more closely link microbial phylogeny and community structure to process rates and controls. In combination with culture-dependent and microscopic approaches, these emerging approaches may

provide a more complete insight into why estuarine microbial communities do what they do, how communities change in response to environmental conditions, and whether the identity of the organisms in the community mix has relevance to the observed community function.

9.3.4 Measuring Microbial Activity

Knowing how many or what kind of microorganisms are present in an estuary does not necessarily provide information about what microorganisms are doing or their rate of activity—abundance and biomass often are not correlated with activity. In addition to knowing how many and what kind of microbes are present, it is essential to have a quantitative understanding of community activity. The ubiquity and the tremendous metabolic diversity of microorganisms in estuaries makes understanding what the community is doing and how fast it is doing it a challenging endeavor; yet, it is a quantitative, mechanistic knowledge of the microbial community that distinguishes microbial ecology from studies on phenotypic and genotypic diversity.

Accurate measurement of microbial metabolism in the natural environment is difficult because most techniques involve manipulation that alters the community's environment sufficiently to alter the rates of a process or even eliminate the process completely. Examples include wall effects observed when a water sample is put in a container or oxygenation of anaerobic salt marsh sediments when removed for study. Effects of manipulation are further exacerbated by the long incubations often required to measure the very low rates of activity that occur in nature. During long incubations, microbes may grow, or die, so that a biased picture of community activity is obtained. Thus, it is critical to evaluate how a selected method affects what is being measured and to design strategies to minimize "sampling effects" and incubation times on community activity.

Hobbie (1993) suggests that a good method for activity measurements (i) deals with microorganisms in their natural surroundings (but does not ignore similar measurements made in laboratory culture), (ii) does not introduce artifacts into the results, and (iii) produces results that are ecologically meaningful within the larger picture, for example, measured rates of nitrogen fixation must fit quantitatively into the overall nitrogen cycle of an estuary. A wide variety of approaches generally satisfy these criteria, depending on the question the investigator is asking; however, it is crucial to keep in mind that there are still some errors associated with nearly every technique used,

and development of more sensitive, rapid, and accurate approaches to measurement of microbial activity is needed.

Microbial ecologists measure what microbes are doing by examining substrates used as carbon and energy sources, electron acceptors and electron donors, and compounds produced by metabolic reactions. When the stoichiometry of a reaction is known, for example, as with denitrification (see nitrogen cycle processes below), measuring specific chemical species provides adequate information to determine what processes are occurring in the environment and, when measurements are made over time, transformation rates can be established. Ideally, activity measurements consider both the types of activities carried out by the community and the rate at which the activity is being carried out. In the remainder of this section, common approaches to measure microbial activity in estuaries are described. Many detailed methodologies are available from sources such as Kemp et al. (1993) or Hurst et al. (2006).

Most activity measurements employ chemical measurement of community metabolism to assess either microbial uptake of materials or transformations of molecules of interest. One of the most common approaches is to use radioactive isotopes to trace the fate of a compound. Techniques relying on radioactive labeling are a highly sensitive way to estimate microbial activity *in situ* and *in vitro*. The basic concept underlying microbial isotope work is simple yet elegant: a sample containing microorganisms is incubated with radioactively labeled compounds, and the cells are collected and analyzed for the amount of radioactivity incorporated. Radioisotope methods are extremely sensitive in that minute amounts of incorporated radiolabel can be detected. Furthermore, depending on the problem at hand, these methods can be "customized" by employing different isotopes (e.g., ^{14}C, ^{35}S, or ^{3}H) to examine assimilation (e.g., ^{14}C-bicarbonate incorporation to measure photosynthesis or chemoautotrophy), respiration (e.g., ^{14}C-acetate mineralization to $^{14}CO_2$), growth rates (e.g., ^{3}H-thymidine incorporation into DNA), or transformations (e.g., $^{35}SO_4^{2-}$ reduction to $H_2^{35}S$).

Stable isotopes have many of the same advantages as radioisotopes, especially those of nitrogen because the radioactive isotopes of nitrogen are so short-lived that it is not feasible to use them *in situ*. Depending on the metabolic pathways involved (reductive vs oxidative), heavy isotopes are discriminated against in favor of lighter isotopes so that the ratio of heavy to light isotopes metabolized is

either depleted or enriched relative to a standard. This process is called *isotope fractionation*. Only reactions mediated by enzymes fractionate, so stable isotopes are often used to determine whether a process is being carried out by microorganisms.

The variety of wet chemical techniques and instruments available to measure the concentration of chemicals in the environment are tremendous, although many techniques lack the sensitivity to detect small concentration changes for compounds present at environmental levels. The disappearance of reactants and/or the appearance of products of a reaction can serve as measures of community metabolism. Depending on the scale of interest, bulk water or soil/sediment samples returned to the laboratory can be analyzed for specific chemical constituents. One of the most useful ways of measuring community activity *in situ* at scales that approach those relevant to individual cells yet with minimal disturbance is with microelectrodes. Microelectrodes are small glass electrodes with tips as fine as 2 μm in diameter. The tips of the electrode are very carefully inserted into the environment of interest and inserted a few fractions of a millimeter at time to follow concentrations of chemicals such as H^+, O_2, N_2O, CO_2, H_2, or H_2S. For example, much of what is known about photosynthesis in benthic microbial mats comes from microelectrode studies.

Using chemical methods singly or in combination, it is possible to estimate values of interest at the community level such as process rates, nutrient and cell turnover rates, growth rates, and death rates (assuming steady-state) to support the ultimate goal of modeling *in situ* community activity.

9.4 ELEMENTAL TRANSFORMATIONS AND ORGANISMS INVOLVED

Thus far, we have addressed the identities, abundances, and patterns of microbial distribution in estuaries. From that discussion comes the logical conclusion that there are many different kinds of microbes and lots of each kind everywhere in estuarine environments. The adage that ''everything is everywhere; the environment selects'' (Baas Becking, 1934, who attributed the idea to passages presented by Martinus Beijerink in the late 1800s) reflects the observation that if there is a function to be performed, microbes will be present and able to carry it out. The more interesting question for microbial ecology is

''What is it that microorganisms do in estuaries?'' As when determining which microbes are where and how many there are, determining what microbes are doing depends on the methods used to answer the question. In estuaries, the large-scale ecosystem processes of production, decomposition, and nutrient cycling are carried out almost exclusively by microbes. Furthermore, these processes are closely linked together, so that each one is heavily dependent on the other two. Although all three processes include both energy transfers and material transformations, the transformations are closely linked by the commonality of the presence of many elements in biomass, that is, biomass composition dictates the reactions and elements involved in biomass synthesis and decay. In particular, conversion of inorganic to organic (i.e., production and nutrient immobilization) and organic back to inorganic (decay and nutrient regeneration) are bound to the dominant element in biomass—carbon (Fig. 9.6). Inevitably, any study on microbial function in ecosystems leads to consideration of the biochemical capabilities of the organisms (material transformations) and cellular energetics.

The following sections describe processes important in nutrient cycles and, to some extent, energetics

Assimilation (biomass synth)
Mineralization(decompostion)
Oxidation (energy)
Reduction (electron acceptor)
Carbon fixation (biomass synth)
Carbon oxidation (energy)
Nitrogen fixation (biomass synth)
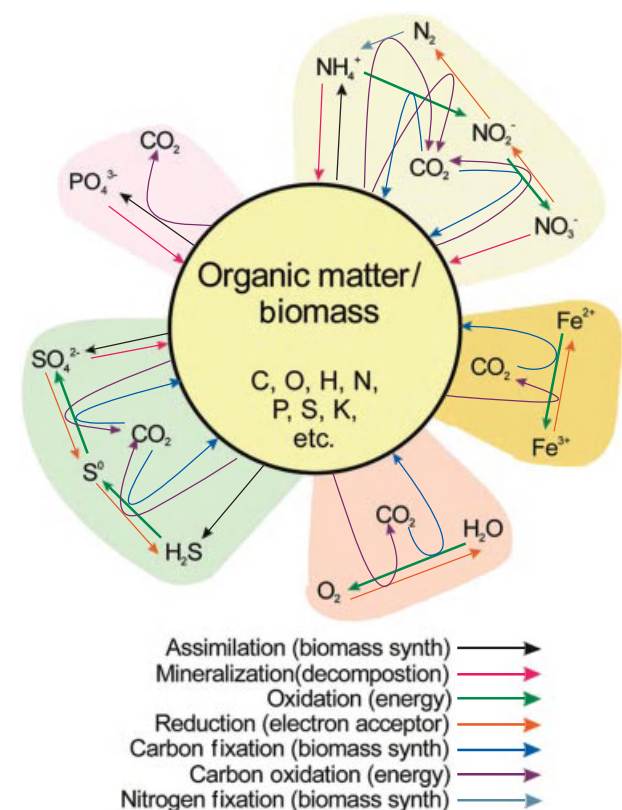
FIGURE 9.6 Material flows in an estuary emphasizing microbial reactions that dominate the processes.

are summarized; the following chapter focuses on the role of microbes in overall energy flow and trophic dynamics. These topics are considered in separate chapters, but it is critical to keep in mind that energy flow and nutrient cycling are intimately linked and cannot be separated. Much more detailed information about the points made below is covered in texts on microbiology, biochemistry, and microbial physiology.

9.4.1 Carbon Fixation and Mineralization

The simplest form of the carbon cycle involves two processes, carbon fixation and carbon mineralization. Microorganisms, including bacteria, play major roles in both processes. The ecological term for carbon fixation is *primary production*. When carbon fixation occurs, CO_2 is converted to organic matter (i.e., biomass) by autotrophic organisms. Autotrophs comprise two major categories, photoautotrophs and chemoautotrophs. The former obtain energy from light and convert it to chemical energy by splitting a reduced molecule (such as H_2O or H_2S) and using the electrons in the synthesis of the energy carrier ATP and the electron carrier NADPH. Photoautotrophs include green plants and macro- and microalgae, but cyanobacteria are also important autotrophs that account for much of the primary production in some locations of estuaries. Cyanobacteria are said to be ''oxygenic photosynthesizers'' such as green plants, because when they use light energy to split water to obtain the electrons, they produce molecular oxygen in the process. There is also a group of photosynthetic prokaryotes called *anoxygenic photosynthesizers* that split H_2S instead of water and produce elemental sulfur rather than O_2 (although some also use H_2, S, a few organics, or Fe(II) as the electron source).

Chemoautotrophs also fix CO_2 into biomass; however, the source of energy for this process is a reduced chemical compound such as NH_4^+, H_2S, Fe(II), or one of several others. In most estuaries, the carbon fixed by chemoautotrophs is less than the carbon fixed by photoautotrophs. But, chemoautotrophic reactions such as ammonium oxidation, sulfur oxidation, and iron oxidation are critical processes in the biogeochemical cycling of elements, including N, S, and Fe, and these processes are intimately linked with the physiological carbon cycle in all environments, including estuaries.

Organisms that use organic carbon formed during primary production are termed *chemoorganoheterotrophs*, or more commonly, heterotrophs. Heterotrophs are responsible for the process of organic decomposition. In general, these organisms use organic compounds as the source of energy, carbon, and electrons. Through mineralization, heterotrophic microbes return elements such as C, N, S, and P that had been incorporated in the organic matter to the environment, a process called *nutrient regeneration*. Heterotrophic activity generates products such as CO_2, NH_4^+, SO_4^{2-}, PO_4^{3-}, and a variety of other mineral compounds and elements.

9.4.2 Nitrogen and Organisms

Nitrogen availability frequently limits primary production in estuarine systems. As a result, when nitrogen enters estuaries in excess, water column production can reach undesirable levels. The consequences are typical of eutrophic systems in that production, death, and subsequent aerobic decay of the producers often depletes dissolved O_2 leading to anoxic conditions that can result in massive fish kills and death of benthic organisms. Much of the concern with estuaries such as the Chesapeake Bay revolves around anoxic or hypoxic (low oxygen) events that kill economically important higher organisms. Most anoxic systems are also associated with unpleasant odors and unsightly accumulations of decaying materials that wash up onto nearby shores. Areas with frequent, persistent anoxic conditions are often termed *dead zones* (Diaz and Rosenberg, 2008), although they are very much alive with active microorganisms.

Complete biogeochemical cycles of a number of mineral elements, for example, N, S, and Fe, are accomplished by the combined action of chemoautotrophs and heterotrophs. Chemoautotrophs use reduced inorganic forms of those elements for energy and electron sources as they oxidize the element. Subsequently, specialized heterotrophic anaerobes use the oxidized forms produced by the chemoautotrophs as electron acceptors for the oxidation of organic carbon compounds resulting in the formation of the reduced forms. The nitrogen and sulfur cycles are excellent examples of this combination of oxidation and reduction reactions (Figs 9.7 and 9.8).

9.4.3 Nitrification

During the decomposition of organic material, nitrogen is mineralized directly from proteins and amino acids as NH_4^+. In oxic environments, however, NO_3^-, and not NH_4^+, is usually the dominant inorganic form of dissolved nitrogen. The conversion from ammonium to nitrate is carried out by the nitrifiers, a group of chemoautotrophic Bacteria and Archaea that mediate the process of nitrification. This conversion
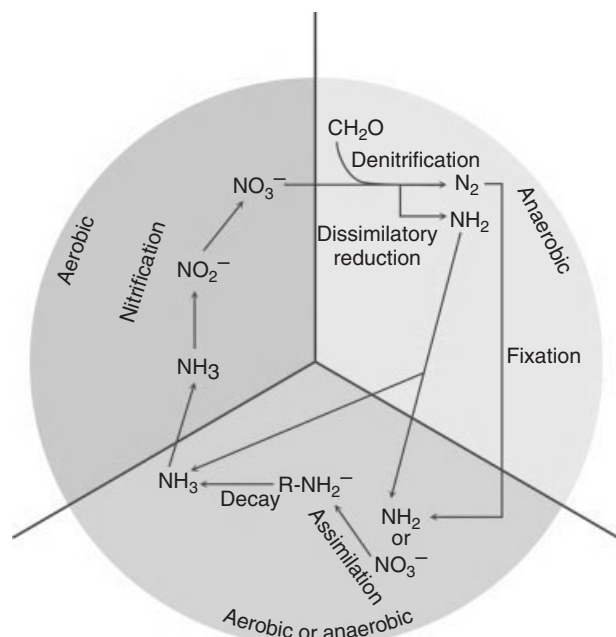
FIGURE 9.7 A generalized view of the nitrogen cycle as it operates in estuaries. A recently documented process of anaerobic ammonia oxidation (anammox) is not shown because it has not been shown to be important in estuarine environments.
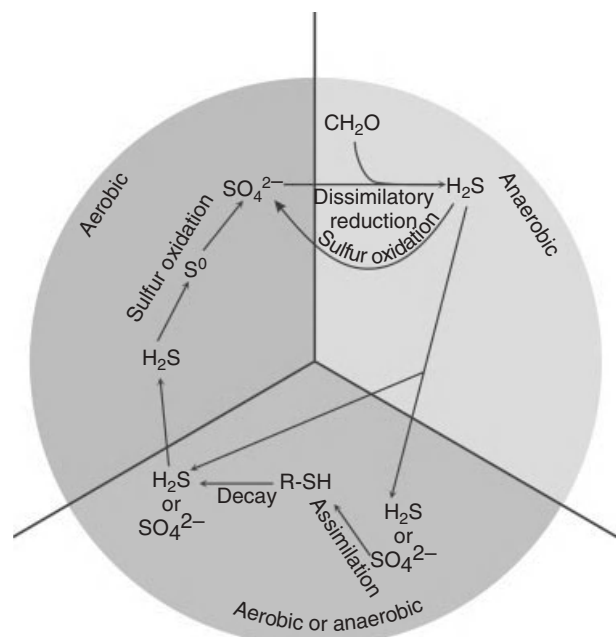
FIGURE 9.8 A generalized view of the sulfur cycle in estuaries. In addition to the shown reactions, microbes generate a series of volatile organic sulfur compounds that are listed in Table 9.4.

is an oxidation reaction, and the nitrifiers are able to trap the energy released during the process for use in biosynthetic reactions. Nitrification occurs in two steps, each carried out by separate types of organisms:

$$NH_4^+ + 3/2O_2 \rightarrow NO_2^- + 2H^+ + H_2O$$
$$(\Delta G = -275 \text{ kJ/mol N})$$
$$NO_2^- + 1/2O_2 \rightarrow NO_3^- (\Delta G = -75 \text{ kJ/mol N})$$
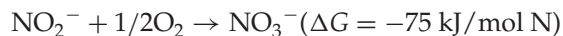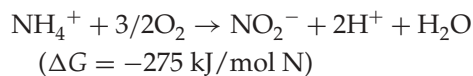
While there are a few different bacteria that carry out each of the two steps, there are none that oxidize ammonium completely to nitrate. There are a few fungi that can oxidize small amounts of ammonium to nitrate, but they do not gain energy from the reaction, and they do not appear to be quantitatively important in any environment. The conversion of ammonium to nitrite is carried out by members of the genera *Nitrosomonas, Nitrosococcus*, and a few others. The isolation of an ammonia-oxidizing Crenarchaeote (putatively named *Nitrosopumilis*) has now been reported (Könneke et al., 2005), and that discovery extends NH_4^+ oxidation beyond a few members of the Bacteria to the Archaea. Although the Crenarchaeota make up a substantial portion of the prokaryote abundance in marine environments, their functions are largely unknown. More recent work suggests that archaea such as *Nitrosopumilis* are as abundant and active at an oceanic scale as in the samples examined by Könneke et al. (2005) and that they are responsible for much of the marine ammonia oxidation (Francis et al., 2005; Moin et al., 2009; Bernhard et al., 2010).

NO_2^- rarely accumulates in the environment, largely due to the activity of the NO_2^--oxidizing bacteria. The lower energy yield per mole of NO_2^- oxidized as compared with ammonium oxidation makes the latter reaction the rate-limiting step in nitrification. The fact that over three times as much NO_2^- must be oxidized as compared with NH_4^+ to obtain the same amount of energy means that, in most cases, NO_2^- is scavenged very efficiently by NO_2^- oxidizers as soon as it is produced. The nitrite oxidizers also comprise just a few types, dominated by the genus *Nitrobacter*.

While substantial amounts of nitrogen-containing gases are generated in the coastal zone by denitrification, it is now known that nitrifiers (particularly NH_4^+ oxidizers) appear to generate copious amounts of the greenhouse gas N_2O as part of their activities (Firestone and Davidson, 1989; de Wilde and de Bie, 2000).

9.4.4 Denitrification

Many microorganisms have the ability to oxidize organic matter either in the presence or absence of oxygen. Organisms that are able to degrade organic matter both aerobically and anaerobically are referred to as *facultative anaerobes*. A large proportion of facultative organisms are able to use NO_3^- as the terminal electron acceptor under anaerobic conditions. The oxidation of organics coupled to the reduction of NO_3^- where N_2 is the reduced product is referred to as *denitrification*. The process using a generic carbohydrate as the carbon/energy/electron source proceeds as follows:

$$6(CH_2O) + 4.8NO_3^- + 4.8H^+ \rightarrow 6CO_2 + 2.4N_2$$
$$+ 8.4H_2O \, (\Delta G = -2671 \, kJ/mol)$$
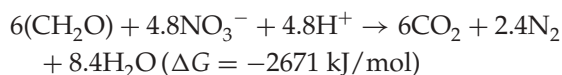
The reactions proceed stepwise generally following the sequence:

$$NO_3^- \rightarrow NO_2^- \rightarrow N_2O \rightarrow N_2$$
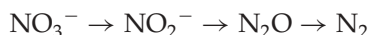
In closed systems (such as sealed flasks in the laboratory where gaseous products are prohibited from escaping), each of the intermediates can often be detected in order, but each is in turn reduced until N_2 is quantitatively recovered. In the environment, the intermediates sometimes accumulate or (in the case of N_2O) escape into the atmosphere and avoid additional biological reaction. Given the large amounts of organic matter produced and received by estuaries and the large amount of nitrate from upland runoff via river inputs to estuaries, denitrification is a major pathway of organic matter degradation in anaerobic waters and sediments, although not as great as sulfate reduction, due to the even greater supply of SO_4^{2-} as compared with NO_3^- in estuarine locations. Indeed, Jørgensen (1980) attributed about half of the organic degradation in coastal marine sediments in a Danish fjord to oxygen respiration and about half to sulfate reduction, with denitrification accounting for <5% of the total carbon mineralization.

Denitrification in estuaries serves as an important filter for nitrogen passing from the terrestrial to the marine environment. Of the 48 Tg NO_3^--N/year entering estuaries from riverine input (Galloway et al., 2004), 10–80% is denitrified, thereby reducing greatly the amount that gets to the ocean. Globally, natural N_2O production is 0.4 Tg N_2O-N/year in estuaries and the coastal ocean. Human activities have at least doubled biogenic N_2O emissions from these regions since 1860, largely as a result of changes in agriculture (Kroeze and Seitzinger, 1998; Seitzinger and Kroeze, 1998; Seitzinger et al., 2000).

9.4.5 Dissimilatory Nitrate Reduction

Some heterotrophs can respire organic matter anaerobically by reducing NO_3^- not to N_2, but rather to NH_4^+. This reaction sequence is referred to as *dissimilatory nitrate reduction to ammonia* (DNRA):

$$6(CH_2O) + 3NO_3^- + 3H^+ \rightarrow 6CO_2$$
$$+ 3NH_3 + 3H_2O \, (\Delta G = -1796 \, kJ/mol)$$
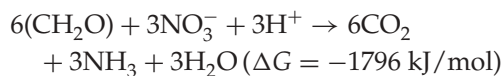
Although the process has been known to occur for many decades, it was thought to be a minor component of the nitrogen cycle in nearly all cases due to the ability of denitrifying heterotrophs to outcompete those that reduce NO_3^- to NH_4^+ (note the higher energy yield using denitrification to oxidize organic matter; Tiedje, 1988). More recent evidence also suggests that denitrification is generally greater than DNRA in most estuarine locations, although in some situations in some locations, for example, surface sediments of some salt marshes, DNRA can be of the same magnitude as denitrification (Koop-Jakobsen and Giblin, 2010).

9.4.6 Nitrogen Fixation

Nitrogen is a major limiting nutrient for primary production in estuaries (see earlier chapters) in part because it is exceeded only by carbon, oxygen, and hydrogen as the most abundant element in plant and animal biomass, and in part because of the predominance of environments in estuaries conducive to denitrification. Even though nitrogen gas (N_2) is abundant in the atmosphere, it is in a form that is unavailable to all but a few prokaryotic organisms, which reduce nitrogen gas to ammonium (NH_4^+). This process is called *nitrogen fixation* and the bacteria carrying out the process are referred to as *nitrogen-fixers* or *diazotrophs*.

The bacteria that carry out nitrogen fixation are a very diverse group that are not closely related phylogenetically and that fix nitrogen under very different types of environmental conditions. Some are autotrophs (e.g., many cyanobacteria), while others are heterotrophs. The one characteristic that all nitrogen-fixing bacteria share is the oxygen-sensitive enzyme, nitrogenase. Nitrogenase is a complex enzyme consisting of several different proteins that are highly conserved (i.e., very similar) from one organism to another. These proteins are rich in Mo,

Fe, Mg, and S, and so all nitrogen-fixing bacteria require these elements in greater amounts than most bacteria. The nitrogen-fixation reaction is as follows:

$$N_2 + 3H_2 \rightarrow 2NH_3, \ \Delta G = +160 \ \text{kJ/mol}$$
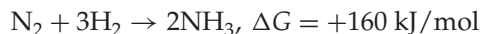
In addition to reducing N_2, nitrogenase reduces a variety of other substrates, including acetylene, allene, cyanide, azide, nitrous oxide, and many others. Because no other enzyme reduces acetylene to ethylene, this reaction can be used to measure the rate of nitrogenase activity using gas chromatography. The acetylene reduction technique is an inexpensive and simple way to estimate nitrogen fixation rates in estuarine samples.

Many nitrogen-fixing bacteria are strict aerobes or are oxygenic photosynthesizers (e.g., the cyanobacteria). Yet, nitrogenase is exceptionally oxygen sensitive and is irreversibly inactivated by O_2. Nitrogen-fixing bacteria have evolved a number of strategies to exclude oxygen or to restrict oxygen contact with nitrogenase. Strategies that are particularly relevant to estuarine bacteria include avoidance, anaerobes and facultative aerobes fix N_2 only in the absence of O_2; microaerophily, some bacteria fix only at low pO_2, so that normal respiration limits the cellular concentration of O_2; clustering, cells grow in dense microcolonies so that cells inside the cluster are protected from O_2 by the respiratory activity; and compartmentalization, the formation of specialized structures for nitrogen fixation, for example, the heterocycts of many cyanobacteria. Overcoming the physiological constraints of O_2 poisoning of the nitrogenase allows nitrogen fixation to occur throughout an estuary under aerobic and anaerobic conditions and all states in between, even by organisms that generate O_2 during photosynthesis.

9.4.7 Sulfur and Organisms

Like nitrogen, sulfur is a plant macronutrient; it is an important component of amino acids and enzyme cofactors. Thus, sulfur is an important component of organic matter. Because of its high abundance in marine habitats (28 mM in the ocean as SO_4^{2-}) sulfur does not limit biological activity in estuarine or marine systems. In general, the sulfur cycle is similar to the nitrogen cycle. Sulfur exists in a variety of redox states, and biological processes either mineralize sulfur, immobilize sulfur through assimilatory sulfate reduction, or transform sulfur from reduced forms (sulfides, thiosulfate, polythionates, and elemental sulfur) to more oxidized forms (sulfates and sulfites) and vice versa (Fig. 9.8). Like nitrogen, reduced sulfur compounds can serve as

energy sources for autotrophic bacteria, and oxidized sulfur compounds can serve as electron acceptors for anaerobic respiration by heterotrophs. However, there are some very important differences. The dominance of these processes and the end products of the reactions are largely determined by environmental conditions. For example, the products of mineralization are sulfate (SO_4^{2-}) under aerobic conditions and H_2S under anaerobic conditions, whereas, regardless of the oxygen status of the environment, the product of organic nitrogen mineralization is always NH_4^+. Furthermore, the lack of a relatively inert species similar in reactivity to N_2 means that no process analogous to nitrogen fixation exists or is necessary. Energetically, therefore, the reductive processes in the sulfur cycle are more conservative in that the product is used directly by chemoautotrophs as an energy source (Howarth and Teal, 1980)

9.4.8 Assimilatory Sulfate Reduction

Most osmotrophic organisms (those that incorporate nutrients by diffusion through their membrane) take up sulfur as sulfate (SO_4^{2-}) and then reduce it to sulfhydryl (HS^-) forms for assimilation into amino acids, principally cystine, cysteine, and methionine. Many sulfur compounds serve as sulfur sources for prokaryotes, including sulfate, hyposulfite, sulfoxylates, thiosulfate, persulfate, sulfide, elemental sulfur, sulfite, tetrathionate, thiocyanate, and organic sulfur compounds, although different microbes use different combinations of sulfur species and no bacterium can incorporate every form of sulfur. Furthermore, many of these compounds are either unavailable to eukaryotic organisms or toxic to them.

9.4.9 Sulfur Oxidation

Just as reduced nitrogen serves as an energy source for some chemoautotrophic bacteria, so does reduced sulfur. The difference is that some of the sulfur-oxidizing bacteria are chemoautotrophs, some are photoautotrophs, and others are facultative autotrophs. One group is completely analogous to the nitrifiers; they obligately oxidize reduced sulfur to provide the energy necessary to fix carbon dioxide. These organisms include members of the genera *Beggiatoa* and *Thiothrix* and some species of *Thiobacillus*. Other members of *Thiobacillus* are facultative autotrophs; they derive energy from reduced sulfur compounds but can utilize organic compounds to supply the carbon for biosynthesis (e.g., *T. novellas* and *T. intermedius*). These two groups of organisms are often referred to collectively as the *colorless sulfur bacteria* to distinguish them from the third group, the photosynthetic

FIGURE 9.9 Extensive covering of a salt marsh sediment surface with purple sulfur bacteria. These organisms are photosynthetic and use H_2S not for energy but as a source of electrons analogous to the use of H_2O for electrons in the light reaction of green plants.

sulfur-oxidizing bacteria that often form green or purple mats on the surface of salt marsh due to the photosynthetic pigments they contain (Fig. 9.9). As the name of this group suggests, the photosynthetic green and purple sulfur bacteria use sunlight to supply the energy for carbon fixation. Instead of using water molecules as a source of electrons during photosynthesis, the green and purple sulfur bacteria use reduced sulfur compounds as a source of electrons. As a result, oxygen is not a by-product of photosynthesis by the green and purple sulfur bacteria and is referred to as *anoxygenic photosynthesis*.

The inorganic compounds of sulfur that are oxidized represent oxidation states from -2 (H_2S) to $+6$ (SO_4^{2-})—an eight electron shift. Not all these transformations require enzymes, but all of them can be enzymatically mediated. Sulfides (HS^-, H_2S), S^0 (elemental sulfur), and $S_2O_3^{2-}$ (thiosulfate) can be oxidized slowly by chemical means, but microbiological oxidation can exceed the equivalent geochemical reaction by around six orders of magnitude under conditions appropriate for microbial growth (Stumm and Morgan, 1996). The colorless sulfur oxidizers are very sensitive to environmental conditions. They are sensitive to hydrogen ion concentrations because they require HS^-, which is favored by circumneutral pHs, so they are found in highly buffered systems such as oceans and estuaries. Chemoautotrophic sulfur oxidizers require an adequate supply of O_2. Because sulfides are generated by sulfate-reducing bacteria (SRB) under anaerobic conditions (see below), sulfur oxidizers must live on the edge at the interface between anaerobic and aerobic conditions exposed

to flooding by sulfate-rich seawater. Salt marshes provide just such an environment and so these organisms are commonly encountered on the surface of salt marsh soils. In the water column, sulfur-oxidizing bacteria can often be found either on the surface of the sediment when the entire water column is aerobic or at the oxic–anoxic interface when the underlying water is anaerobic. Because sulfur oxidizers are chemolithoautotrophs, they do not require organic carbon for their growth and are not involved in carbon mineralization in a direct way. Most are aerobes, but some, including *Thiobacillus denitrificans*, can grow anaerobically using nitrate (NO_3^-) as a terminal electron acceptor (oxidizing agent).

These organisms carry out the following reactions:

$$HS^- + H^+ + \tfrac{1}{2}O_2 \rightarrow S^0 + H_2O,$$
$$\Delta G = -209 \text{ kJ/mol S}$$
$$S^0 + 1.5O_2 + H_2O \rightarrow 2H^+ + SO_4^{2-},$$
$$\Delta G = -628 \text{ kJ/mol S}.$$
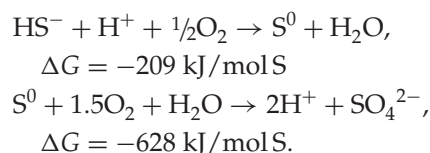
Thiobacillus thiooxidans and *Thiobacillus ferroxidans* (recently renamed *Acidthiobacillus*) are interesting organisms. Together they oxidize S and Fe^{2+} found in metal sulfides such as pyrite (FeS_2), which is common in many salt marshes. The reactions that these organisms carry out sum to the following:

$$4FeS_2 + 15O_2 + 14H_2O \rightarrow 4Fe^{3+}$$
$$+ 3OH^- + 16H^+ + 8SO_4^{2-}$$
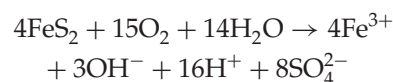
which yields energy to both organisms.

The photosynthetic sulfur oxidizers are also sensitive to environmental conditions. The conundrum they face is the combined requirement for reduced sulfur produced under anaerobic conditions and sufficient light to support carbon fixation. Consequently, the photosynthetic green and purple sulfur bacteria are most abundant on the surface of salt marsh soils and sediments receiving sufficient light to support photosynthesis. These organisms carry out the following reactions:

$$CO_2 + 2H_2S + \text{light energy} \rightarrow$$
$$CH_2O + 2S^0 + H_2O$$
$$CO_2 + S^0 + 2H_2O + O_2 + \text{light energy} \rightarrow$$
$$CH_2O + 2H^+ + SO_4^{2-}.$$
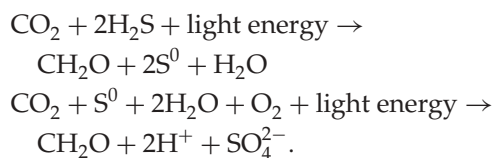
The significance of sulfur oxidation in estuaries is that the ultimate end product of the process is sulfate (SO_4^{2-}), a nontoxic sulfur form highly abundant in marine systems of all kinds. Indeed, Lavik et al. (2009)

credit chemoautotrophic sulfur oxidation with detoxifying sulfidic waters in parts of the open ocean, making the surface waters overlying sulfide-rich areas habitable for fish and other nekton. Rates of sulfur oxidation vary widely among estuarine habitats; oxidation of H_2S in Chesapeake Bay range from minutes near the sediment surface in deep water to hours in surface water (Millero, 1991). In addition, sulfate plays a critical role in anaerobic mineralization of the organic matter, especially in salt marshes. We discuss this important process and the organisms carrying out the process in the following section.

9.4.10 Dissimilatory Sulfate Reduction

Most osmotrophic organisms take up $SO_4{}^{2-}$ and reduce it to HS^- for assimilation into biomass rather than using free H_2S, which is toxic to many organisms. Some prokaryotes, however, can use $SO_4{}^{2-}$ as a terminal electron acceptor for the oxidation of organic matter. This process is referred to as *dissimilatory sulfate reduction* to distinguish it from sulfate uptake and reduction for assimilation. Most of the sulfides (H_2S, HS^-, metal sulfides, etc.) that accumulate in estuaries are produced via dissimilatory sulfate reduction, although anaerobic mineralization of organic sulfur compounds leads to the same product (e.g., mineralization of the amino acids methoinine and cysteine). Like the bacteria carrying out the analogous process in the nitrogen cycle (denitrifiers), the SRB are heterotrophs. In contrast to the diversity of denitrifiers, however, there are just a few types of SRB. In addition, SRB are all obligate anaerobes, whereas the denitrifiers are mostly facultative. While the presence of oxygen slows, or even stops, denitrification, the organisms continue to respire using oxygen. The presence of O_2 also halts sulfate reduction; however, the SRB only tolerate oxygen, that is, O_2 does not kill the bacteria, but it does prevent the SRB from mineralizing organic matter. When anaerobic conditions reoccur, sulfate reduction recommences.

Several SRB exist with a variety of physiologies. The most commonly studied organisms are *Desulfovibrio* spp.—nonspore forming obligate anaerobes that produce H_2S from $SO_4{}^{2-}$ rapidly. However, Leloup et al. (2007) suggest that in some sediments, sulfate reduction is largely carried out by a very diverse group of heretofore uncultured SRB. The reaction SRB carry out is as follows:

$$2(CH_2O) + SO_4{}^{2-} + 2H^+ \rightarrow H_2S + 2CO_2 + 2H_2O.$$
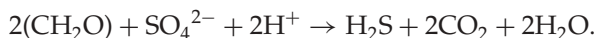
Because dissimilatory sulfate reduction is a heterotrophic process, it is enhanced by the addition of organic materials. The process also depends on an adequate supply of sulfate and can be limited in salt marsh soils regularly inundated by full strength seawater, even though the concentration of sulfate in seawater is typically 28 mM. In natural settings, acetate, lactate, and volatile fatty acids are the most common energy source used by the SRB (Finke et al., 2007). Thus, SRB are dependent on the activities of fermenting microorganisms that convert complex carbohydrates and sugars to the low molecular weight organic acids.

In the largely anaerobic sediments and soils of estuaries, dissimilatory sulfate reduction is an extremely important process. SRB pass energy from plants to food chains based on reduced sulfur. During the reduction of $SO_4{}^{2-}$, some of the chemical energy from the organic compounds is transferred to the sulfide. When the sulfide is then oxidized by chemoautotrophic sulfur oxidizers, the CO_2 that is fixed becomes part of the organic pool that can ultimately support production in higher trophic levels (Howarth and Teal, 1980). Well over half the organic matter mineralized in salt marsh sediments occurs via dissimilatory sulfate reduction (Jørgensen, 1980; Howarth and Hobbie, 1982; Howes et al., 1984).

9.4.11 Volatile Sulfur Compounds

Attempts to characterize the global cycling and behavior of sulfur in the atmosphere in the 1980s suggested the importance of marine and estuarine microbes in the production of volatile sulfur, particularly in salt marshes. Salt marshes are an ideal environment for the formation of volatile sulfur compounds because the soils are anaerobic just a few centimeters to a few millimeters below the surface, are rich in organic materials, and $SO_4{}^{2-}$ is replenished each time the soils are flooded. Those volatile sulfur compounds that enter the atmosphere are eventually oxidized to sulfur dioxide (SO_2) and sulfate ($SO_4{}^{2-}$) and contribute to the acidification of precipitation (Andreae and Jaeschke, 1992). Several key steps in the nitrogen cycle are adversely affected by sulfur gases or their atmospheric alteration products—for example, the cyanobacteria are more sensitive to $HSO_3{}^-$ than algae or heterotrophs and nitrification may be retarded by methanethiol, DMS, and H_2S.

A variety of volatile sulfur compounds are biogenically produced (Table 9.4). Of these, H_2S and DMS are the dominant gases released to the atmosphere (Giblin and Wieder, 1992). Hydrogen sulfide is produced during dissimilatory sulfate reduction as described above, and volatile organic sulfur compounds such as DMS and methanethiol are produce during the decomposition of sulfur-containing

TABLE 9.4 Volatile products of microbial sulfur cycling

Sulfur gas	Name	Release to the atmosphere from salt marshes (Tg/year)
H_2S	Hydrogen sulfide	0.8–0.9
CH_3SCH_3	Dimethylsulfide (DMS)	0.58
H_3CSSCH_3	Dimethyldisulfide (DMDS)	0.13
H_3CSH	Methanethiol	ng
CH_3SCOCH_3	Methane thioacetate	ng
C_2H_6S	Ethanethiol	ng
$C_4H_{10}S_2$	Diethyl disulfide	ng
CS_2	Carbon disulfide	0.07
COS	carbonyl sulfide	0.12

Abbreviation: ng, not given.
Source: Estimates of annual emissions to the atmosphere are from the study by Lomans et al. (2002).

organic molecules, including dimethylsulfonio-propionate (DMSP), an osmolyte in many algae, dinoflagellates, and marsh plants (Dickson et al., 1980; Dacey and Blough, 1987; Turner et al., 1988; Lomans et al., 2002). Indeed, genes for DMSP metabolism are present in a wide variety of highly abundant marine organisms (Howard et al., 2008), and the DMSP molecule is considered to be one of the most important in the marine cycling of sulfur through planktonic microbes (Kiene et al., 2000).

Emissions of volatile sulfur compounds from estuarine habitats are highly variable both spatially and temporally (Table 9.4; Giblin and Wieder, 1992) and are only a small fraction of the global sulfur budget; 1–2% of the 78.9–142.6 Tg S produced each year (Andreae, 1984; Lomans et al., 2002). A variety of factors influence volatile sulfur emissions, including temperature (Hicks and Lamontagne, 2006), diurnal cycles (Cooper et al., 1987; Demello et al., 1987), soil saturation (Peterson et al., 1983; Steudler and Peterson, 1985), salinity (DeLaune et al., 2002a,b), soil sulfate content (DeLaune et al., 2002b), and soil texture (Cooper et al., 1987). These factors affect microbial activity, as well as abiotic sulfur reactions.

9.4.12 Iron, Manganese, and Organisms

Both iron and manganese are highly reactive elements that are cycled through various redox states by a combination of biological and abiological processes. Oxidation and reduction reactions for these elements are quite common, with O_2 being the dominant electron acceptor for oxidation (NO_3^- has also been implicated along with chlorate and perchlorate in some contaminated environments, Weber et al., 2006). Reduction of Fe^{3+} and Mn^{4+} is largely a process in which the metals serve as the electron acceptor for the oxidation of a variety of organic and inorganic compounds. In anoxic estuarine sediments, sulfide

abiotically reduces Fe^{3+}, but there is ample evidence that some microbes capture energy using iron as the electron acceptor during anaerobic carbon oxidation:

$$Acetate^- + 8Fe^{3+} + 4H_2O \rightarrow 2HCO_3^-$$
$$+ 8Fe^{2+} + 9H^+, \Delta G = -233 \text{ kJ}$$
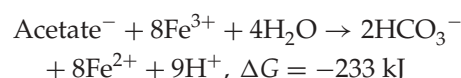
in which the energy yield is calculated for the use of acetate as the electron donor/energy source (after Froelich et al., 1978).

In the oxidation of iron, the energy yield per mole of iron oxidized is quite low,

$$Fe^{2+} + \frac{1}{4}O_2 + 5/2H_2O \rightarrow Fe(OH)_3 + 2H^+,$$
$$\Delta G (\text{pH } 7) = -18 \text{ kJ}$$
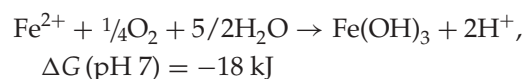
but the abundance of iron in the environment is high, and it is readily recycled by microbial reduction to Fe(II) from Fe(III). Thus, by oxidizing a large amount of iron, iron-oxidizing chemolithoautotrophs can exploit the small amount of energy released by the reaction to fuel their biosynthesis and growth.

At circumneutral pH, iron exists predominantly as Fe(III), and the conversion from Fe(II) occurs rapidly even in the absence of microbial activity. Because the pH of the ocean and most estuarine habitats is at or above pH 7, biological iron oxidation may not be a quantitatively important process. Iron-oxidizing bacteria in estuaries are not as well studied as their terrestrial counterparts. Because of the strong pH buffer found in brackish-water systems, the common acidophilic Fe oxidizers such as *Acidithiobacillus ferrooxidans* are uncommon. Nevertheless, some strains that oxidize iron under circumneutral pH conditions have been identified and recovered from estuaries. For example, *Gallionella* spp. are organisms that become coated in iron-oxide precipitates as they grow (Fe^{3+} rapidly hydrolyzes to the insoluble $Fe(OH)_3$ at circumneutral pH). The habitat most conducive to iron oxidation in estuaries would be

a microaerophilic one (very low oxygen) such as at the interface of the oxic and anoxic zones. Such a habitat would offer a juxtaposition of conditions that would promote iron reduction with those that would allow iron oxidation (i.e., presence of reduced iron and oxygen). One such habitat is the exposed surface of the sediment of marshes where, under anaerobic conditions, Fe(II) compounds may exist, especially as products of anaerobic iron reduction.

Another habitat where Fe oxidation is observed is the rhizosphere of salt marshes, where plants often create a sharp oxic–anoxic interface in association with their roots. Iron oxidation can occur biologically or abiologically on or very near the root surface where O_2 penetrates an otherwise anoxic environment. The proximity of an oxidizing zone immediately adjacent to anaerobic sediments makes an ideal habitat for rapid cycling of iron, both oxidative and reductive processes. Organisms suited to a wide range of macroenvironments can cycle iron in the rhizosphere. For example, King and Garey (1999) compared two strains of iron-reducing bacteria, one from macrophyte roots in fresh water sediments and one from roots of marine macrophytes. Their results indicated that while the two isolates were quite similar in many of their characteristics, iron reduction by the fresh water isolate decreased with increasing salinity, while reduction by the marine isolate displayed a relatively broad optimum salinity between 20 and 35 psu.

Shewanella spp. may be the dominant iron-oxidizing organisms in estuarine and marine systems. Although these organisms are considered marine, members of the genus are widespread, and are frequently recovered from soil and fresh water, as well as from estuarine and marine habitats, and they have even been implicated in septicemias (bloodstream infections). The organism has been known for some time and the type species was originally referred to as *Pseudomonas putrifaciens*.

In marine systems, most commonly in oceanic habitats as opposed to estuarine environments, the oxidation of Mn(II) to Mn(IV) is frequently observed. In fact, at oceanic sediment surfaces, the reaction can result in the formation of concretions (nodules) that contain both Fe and Mn. While nodules can be found widely in soils and lakes, those in active areas of the sea floor are commonly 5–10 cm in diameter. Although the oxidation of Mn yields energy (Erlich, 1978),

$$Mn^{2+} + 1/2O_2 + H_2O \rightarrow MnO_2 + 2H^+,$$
$$\Delta G = -68.2 \text{ kJ}$$
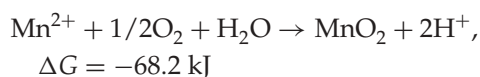
many of the organisms that carry out the reactions are heterotrophs, including *Bacillus* spp., *Pseudomonas*

spp., *Leptothrix* spp., and some fungi as well as a number of other organisms in the Proteobacteria, Firmicutes, Actinobacteria, and several organisms not included in any of these groups (Tebo et al., 2004). It is not clear how, or even if, the organisms take advantage of the potential for energy gain by conducting this reaction. In estuarine habitats, the most likely place to find Mn oxidizers is at the oxic–anoxic interfaces where a supply of both Mn(II) and O_2 might be present (Tebo et al., 2004). In that location, as occurs for iron cycling, both oxidation and reduction of manganese can occur in close proximity.

As with iron and a number of other inorganic redox species, Mn reduction serves as an electron sink for the oxidation of organic matter (primarily) and some inorganics (probably to a much lesser extent). Although little is known about manganese reduction in marshes and estuaries, the observation of similar porewater concentrations of Fe^{2+} and Mn^{2+} suggests that rates of reduction might be similar. Indeed, the primary control on rates of reduction of both iron and manganese may be the relative availability of the reactive oxides in the solid phase (Joye et al., 1996). Like iron, manganese can be both oxidized and reduced abiotically; Joye et al. (1996) reported that half of the manganese mobilization (reduction of insoluble MnO_2 to the soluble Mn^{2+}) in microbial mats in a Georgia salt marsh was biological. Continued examination of both iron and manganese is needed to delineate the exact microbial role with respect to each in the biogeochemistry of estuarine marshes.

9.4.13 Phosphorous and Organisms

The phosphorus cycle in estuaries is much simpler than any of the elements discussed so far because phosphorus does not serve as an electron acceptor or donor during microbial metabolism. As a result, the cycle can be summarized simply as one of assimilation and mineralization. Nevertheless, the phosphorus cycle is regulated both directly and indirectly by the activity of microorganisms. Because phosphorus is so biologically and chemically reactive, the residence time of dissolved phosphate is short (Pomeroy, 1960). Inorganic dissolved phosphate is biologically immobilized by autotrophic and heterotrophic micro- and macroorganisms. Physical–chemical processes, especially sorptive interactions with sediment particles, remove dissolved phosphate from the water column (Welsh, 1980). Release of inorganic phosphate into the water column may result from biological processes in the sediments.

Phosphate is taken up and released biologically and abiologically by both aerobic and anaerobic sediment, although more exchange occurs between water

and anaerobic sediments. Exchange is greater if sediments are disturbed than undisturbed (Pomeroy et al., 1965). As oxygen slowly diffuses into sediments, it is rapidly consumed by sediment microorganisms. As the oxygen concentration is depleted with depth, dissimilatory sulfate reduction dominates, producing sulfide, which decreases the redox potential, causing dissolution of reactive iron and manganese phosphates and release of inorganic phosphate to the water column (Froelich, 1988; Chambers and Odum, 1990; Thamdrup et al., 1994; Kemp et al., 2009). In addition, active reduction of the iron and manganese compounds (often oxides) by microbes can greatly accelerate the release of phosphorus by this means. If the surface of the sediment remains aerobic, much of this phosphate is again made insoluble as it diffuses, or is mixed by bioturbation, into the aerobic zones. If the overlying waters are anoxic, however, the phosphate may enter the water column, stimulating photosynthesis. Thus, the availability of inorganic phosphate to estuarine phytoplankton depends on indirect and direct microbial processes in the water and sediments.

9.5 MICROBES AND ECOSYSTEM PROCESSES

Organisms as small as microbes can have ecosystem-level impacts because they are so abundant and the processes they mediate occur so rapidly. Throughout this chapter, the importance of microbes to estuarine ecosystems has been implicit. This section provides an overview of the kinds of landscape-scale characteristics of ecosystems affected by microorganisms.

9.5.1 Nutrient Cycling

Many of the transformations described previously are uniquely microbial, while for others, the rates are controlled by microorganisms, even though the microbes do not directly catalyze the reactions. For example, microbial oxygen consumption during organic matter decay can control the rate and extent of phosphorus complexation with iron. The carbon, nitrogen, sulfur, oxygen, and phosphorus cycles are strongly regulated, as are the cycles of many metals, both directly and indirectly by microbes.

None of the processes we have described occurs in isolation. Where reduction of an element occurs, the reaction must be coupled to an oxidation. It is the coupling of oxidation and reduction (redox) reactions that leads to the cyclical nature of many ecosystem

nutrient transformations. The redox cycles of both nitrogen and sulfur by assemblages of heterotrophs and chemoautotrophs represent excellent examples of this phenomenon. In other cases, for example, phosphorous, oxidation and reduction of the P atom does not occur, but uptake and release of PO_4^{3-} by organisms is controlled by the accumulation of biomass based on energy trapped from oxidations of other reduced elements. The energy driving those reactions is ultimately derived from sunlight or from reduced inorganic compounds, which have either geological origins or which contain solar energy captured biologically and stored temporarily. It is the balance of these redox processes that result in observed ecosystem nutrient cycling.

9.5.2 Productivity

Microbes regulate rates of ecosystem primary production directly and indirectly: while many make nutrients available through mineralization, other microbes are primary producers themselves, and they compete with plants and macroalgae for inorganic nutrients. When light is available, both oxygenic and anoxygenic photoautotrophs contribute to primary production. Photoautotrophs tend to dominate prokaryotic primary producers at the ecosystem level contributing between 2% and 28% to the total chlorophyll-*a* pool in the estuarine water column (Teixeira and Gaeta, 1991; Iriarte, 1993; Sin et al., 2000); locally, however, chemoautotrophic primary producers, those using reduced inorganic compounds for reducing power, can be an important source of organic matter (Kristensen and Hansen, 1995; Evrard et al., 2008).

Microorganisms are also important secondary producers. In estuaries, there is a positive relationship between bacterial abundance and protozoan grazers and between bacterial growth and protozoan grazing rates (Sanders et al., 1992). Protozoa are directly involved in aquatic food webs as an intermediate link between bacteria and zooplankton. Thus, when bacteria are grazed by protozoa, bacterial biomass enters the food web—a microbially based food web (a topic covered in Chapter 10)—and some primary production that might otherwise be lost from the ecosystem as CO_2 through mineralization of dead primary producers remains in the ecosystem as bacterial cells. As a result of the retention of microbial community secondary production within the system, energy and organic matter may be conserved for macrofauna and eventually harvested by humans.

9.5.3 Organic Matter and Decomposition

Carbon is arguably the single most important element in estuaries. For example, plants and microbes are

approximately 40–50% carbon on a dry weight basis. Higher animals are as well if the bony skeleton is ignored. High fishery production is related to organic matter (Nixon, 1980; Day et al., 1989), and a major part of energy flow in most estuaries is based on organic matter. In fact, more organic matter is processed per unit area in estuaries than any other type of ecosystem (Odum, 1983).

Decomposition of organic matter is one of the key functions for maintenance of estuarine ecosystems. During decay of organic matter, inorganic compounds are released that can be used by autotrophic and heterotrophic macro- and microorganisms to support their growth. While decomposition is an integrated process involving physical, chemical, and biological forces, it is performed primarily by heterotrophic microorganisms. Microbial processes and community diversity (evenness and richness) are controlled by many factors, including organic matter quality (susceptibility to decay), substrate particle size, edaphic conditions, and climate. Advances in molecular, especially genomic, methods have revealed large numbers of new and interesting microbes in estuaries, and assigning those organisms to specific functions represents the next major challenge for estuarine microbiologists.

The organic matter in estuaries comes from several sources: phytoplankton, terrestrial, salt marsh plants, and aquatic plants, as well as animal carcasses and waste products. The chemical and physical heterogeneity of organic matter sources is a reflection of the diversity of sources and the complexity of the biochemicals composing living things. As organic matter decays, the water-soluble fractions are lost rapidly, generally within several days of death of the primary producer, and the percentage of other materials rises (Fig. 9.10). Valiela et al. (1984) referred to this stage of decay as the *leaching phase*. Both labile (rapidly mineralized) and refractory (slowly mineralized) compounds are leached from the organic matter. There is often an initial decrease in the nitrogen content (Odum and de la Cruz, 1967) that corresponds to a rapid increase in bacterial biomass (Blum and Mills, 1991). The second stage of decay, the decomposer phase, occurs more slowly as fungi and bacteria colonize the tissues and begin to mineralize easily metabolized detrital constituents such as cellulose and hemicellulose. Loss of cellulose and hemicellulose results in weakening of the fibrous tissues and they are broken into smaller pieces. Mechanical grinding of the tissues by amphipods, grass shrimp, and other macrofauna reduces the particle size and increases the surface area for further microbial colonization. As the percentage of the cellulosic
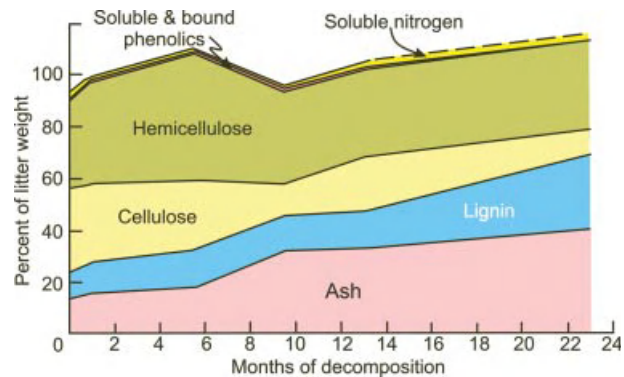
FIGURE 9.10 Cumulative percentage of the major chemical constituents of *Spartina alterniflora* litter during decay. *Source:* Figure redrawn from Valiela et al. (1984).

materials falls, the percentage of recalcitrant compounds increases and decomposition slows. During the final stage of decay, the refractory phase, very complex, difficult to degrade materials remain (lignin, waxes, resins, and pigments) and decay proceeds even more slowly than in the second stage. All particulate organic matter, regardless of the source, follows this general scheme, although the rates of decay vary widely depending on the organic matter characteristics and environmental conditions. Dissolved organic matter also follows the pattern of rapid decay of labile fractions followed by a slower breakdown of refractory compounds.

Many environmental factors regulate the rate of decomposition and the processes described above. Temperature and oxygen (or other terminal electron acceptor) availability are most frequently noted as the primary regulating factors. Other factors affecting decomposition include organic matter nitrogen content and particle size. All these factors are interrelated and the impact of one is often determined by the condition of the others.

Temperature regulates the rates at which metabolic processes occur, including decomposition, and is a determinant of community structure through its impact on the growth of individual populations. Increases in temperature are typically accompanied by increases in process rates over the range of temperatures supporting microbial growth. Many studies have focused on seasonal effects that are most often related to temperature changes. The latitudinal differences in climatic temperature should alter the nature of microbial communities, but direct, systematic, comparative studies on microbial processes and community structure in estuaries with different climates are rare (Newell et al., 2000; Blum et al., 2004).
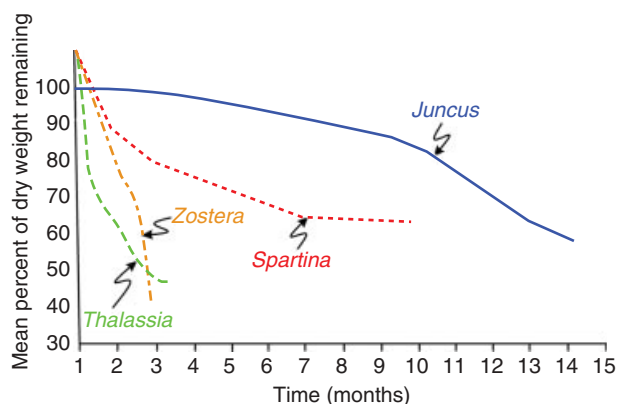
FIGURE 9.11 Comparison of the degradation rates of detritus derived from Juncus (Heald, 1969), Thalassia (Zieman, 1975), Zostera (Burkholder and Doheny, 1968), and Spartina (Odum and de la Cruz, 1967). *Source:* Figure redrawn from Day and Christian (1989).

The presence or absence of oxygen has a major impact on which of the metabolic processes described will occur and is a determinant of community structure (Jørgensen, 1980). Aerobic organisms flourish in the presence of oxygen. As oxygen concentration decreases within a habitat, the oxidation–reduction potential (Eh) becomes controlled more by the presence and state of elements other than oxygen. Oxygen, nitrate, ferrous iron, sulfate, carbon dioxide, and some organic molecules (e.g., pyruvate and acetaldehyde), in this order, can be used as terminal electron acceptors by various bacterial populations to decompose organic matter. Heterotrophic microbes respiring using nitrate, ferrous iron, sulfate, and carbon dioxide in respiration (anaerobic respiration) and fermenting microbes dominate the community in the absence of oxygen. Thus, microbial community structure and the processes the community carries out are altered dramatically with increasing depth in the water column and the sediment (e.g., Jørgensen, 2006; Lin et al., 2007; Glud, 2008).

Organic matter in estuaries tends to have a high ratio of carbon to nitrogen (typically exceeding 20:1). Since microbes have a C:N ratio of approximately 10:1, a source of inorganic nitrogen may be required for growth. Both oxidized (NO_2^- and NO_3^-) and reduced (NH_4^+) forms of nitrogen are good external sources of nitrogen for microbes. The assimilation of inorganic nitrogen (as well as other plant macronutrients, e.g., P, K, and Ca) from the microbes' environment during the assimilation of organic carbon can reduce the quantity of plant-available nutrients such that these nutrients are limiting to plant growth. Because microbial immobilization of nutrients is proportional to the amount of carbon

assimilated by microbes, the C:N, C:P, C:K, etc. ratios of organic matter in estuaries becomes an important factor in nutrient cycling. Generally, organic materials with low C:N ratios are decayed more rapidly than those with high C:N ratios; however, there are notable exceptions—for example, the simple sugars ($C_6H_{12}O_6$) that turn over very rapidly in estuaries. Thus, that *J. roemerianus* decays more slowly than *Spartina alterniflora* or the seagrasses, *Zostera marina*, and *Thalassia testudinum* would be predicted based on the C:N (65:1, 35:1, 30:1, and 25:1, C:N ratio, respectively) of these plant tissues (Fig. 9.11).

9.6 SUMMARY

Communities of microorganisms and the processes they carry out exhibit temporal and spatial complexity in estuarine ecosystems that is only just beginning to be understood. Many of the important questions remaining to be answered about microbial communities in estuaries are dependent on the availability of appropriate techniques. What is known about microbes is that they are more abundant, diverse, and active in estuaries than any other group of organisms. They are major participants in all the important ecosystem functions such as nutrient cycling, photosynthesis, and decomposition. Many of the biological transformations of the carbon, nitrogen, and sulfur cycles are uniquely microbial. These processes were occurring two billion years before present, or more, and at least one billion years before plants and animals evolved (Margulis and Dolan, 2002). The early evolution of microorganisms, especially the Bacteria and Archaea, allowed them to become extremely diverse. As a consequence, they contribute to ecosystem biogeochemical resilience, trophic dynamics, and resistance to invasion. Although microbial communities are diverse and the numbers of individuals in the community are large, not all individuals are active at any given time or place as a result of variation in the physical, chemical, and biological characteristics of estuary. This variation gives rise to differences in microbial community composition, which processes are carried out, and at what rate the processes occur.

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ESTUARINE MICROBIAL FOOD WEBS

Byron C. Crump, Hugh W. Ducklow, and John E. Hobbie

10.1 INTRODUCTION

The organisms of planktonic ecosystems organize in an intricate food web; carbon and energy pass from one functional level to another in a well-ordered system following rules of function and size for primary producers, consumers, and decomposers. Until the 1970s and 1980s, the prevailing ecological scheme showed carbon and energy, packaged by phytoplankton, moving through the food web as particles and organisms. Since then, scientists have realized that bacteria and dissolved organic carbon (DOC) must be added to the scheme as major components of the planktonic food web. The smallest organisms of the planktonic food web, viruses, bacteria, algae, and ciliates, make up the microbial food web along with particulate and dissolved organic matter (DOM).

An idealized scheme of carbon flow through a planktonic food web (Fig. 10.1) emphasizes two different modes of carbon transfer: as particles, which are consumed by phagotrophic organisms that directly ingest particles, and as DOC that is consumed by bacteria. In this ocean food web, DOC is produced by phytoplankton during photosynthesis and during their decomposition. It is also released during the process of phagotrophy as flagellates, ciliates, and other organisms crush, eat, and digest particles. Bacteria recover DOC, and these bacteria, in turn, are consumed by phagotrophs.

A critical role of heterotrophic bacteria in natural ecosystems is the remineralization of organic matter (OM; see Chapters 3 and 9). Bacteria oxidize organic carbon and recycle organic nitrogen, phosphorous, and other nutrients into inorganic forms for subsequent uptake by primary producers. But it turns out that bacteria do not carry out these processes by themselves. While bacteria remineralize a portion of their OM diet, they also convert a significant fraction into new bacterial biomass. So it falls to the bacterivores (organisms that graze on bacteria), mainly heterotrophic nanoflagellates, and to predators on the bacterivores to digest bacterial biomass. As a community, these organisms cooperate in remineralization, oxidizing most of the OM they consume. In this way, the microbial food web acts as a so-called sink for OM.

But this bacteria-based community can also function as a microscopic food chain that transfers materials and energy from nonliving OM through bacteria to higher trophic levels. Incubation experiments using ^{14}C as a tracer of bacterial biomass confirm that bacteria can contribute to the diet of zooplankton such as copepods and rotifers (Havens et al., 2000; Work et al., 2005). How important bacterial biomass is in this diet remains a subject of debate, but in this way, the bacteria-based microbial food web links higher trophic levels to DOM.

Microbial food webs are best described for purely pelagic, stable, and self-contained ecosystems such as the open ocean, where the organisms involved are
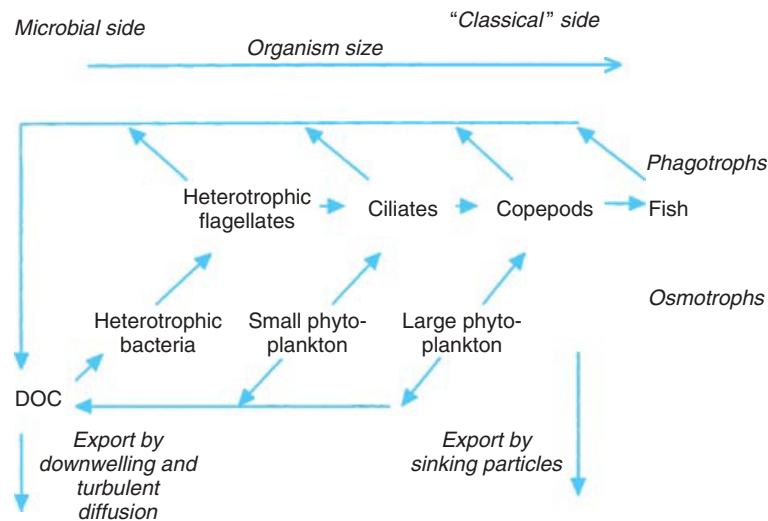
FIGURE 10.1 Idealized scheme of carbon flow in a planktonic food web. *Source:* Figure 2 in Thingstad (2000).

all planktonic, nutrients are scarce, and the main OM supply is phytoplankton. In contrast, most estuaries are anything but purely pelagic, being often very shallow and heavily influenced by benthos, marshes, and seagrass beds. They are also anything but stable, often having energetic hydrodynamics, limited water residence times, and strong gradients in salinity, nutrients, and oxygen. And finally, they are anything but self-contained, receiving material inputs from both land and the coastal ocean.

In this chapter, we summarize our current understanding of the standard oceanic microbial food web and then adapt that paradigm to the estuarine environment, describing how it is modified in estuaries by elevated primary productivity, multiple sources of OM, limited residence time, changes in the abundance and types of grazers, interactions with sediments and other surfaces, and strong gradients in temperature and salinity.

10.2 THE MICROBIAL FOOD WEB OF THE OCEAN

Much of the research on microbial food webs has been carried out in the pelagic ocean where there is no influence from land, all the organisms are planktonic, nutrients are scarce, and the main OM supply is phytoplankton. We describe this food web of the oligotrophic ocean in the following sections.

10.2.1 The Organisms

Bacteria in the plankton typically look like small spheres or rods with a diameter of 0.5 μm or less. In this habitat, almost all bacteria function as osmotrophs. They release enzymes that break down complex organic particles and DOC to simple compounds such as sugars, amino acids, and fatty acids. The bacteria then transport these compounds through their cell wall.

Bacteria are present in ocean waters at around 1 million cells/ml. When several milliliters of ocean water are filtered and the bacteria caught on the filter are observed with a fluorescent stain (Fig. 10.2), they appear to be abundant. Yet in the water, each tiny cell is actually spaced about 100 μm from adjacent cells.

Flagellates are the next larger members of the microbial community. They are generally 2–20 μm in diameter or length. As pictured in a laboratory culture in Figure 10.3, they move by flagellae, and feed by engulfing bacteria they encounter as they move through the water. Many flagellates are purely heterotrophic, while others live only by photosynthesis. The group of flagellates represented by the chrysophyte seen in Figure 10.3 actually carries out both processes; they are called *myxotrophs*. Flagellates are much less abundant than their prey, the bacteria. In the ocean their numbers are around 10^3/ml or only one thousandth that of the bacteria.

Ciliates are an order of magnitude larger than the flagellates and small algae they feed upon. The organism shown in Figure 10.4 is about 80 μm in length and has been feeding on small diatom cells. These protists move by cilia and ingest particles through a mouthlike structure. Ciliates are even less abundant than flagellates, 1–10 cells/ml.

Another component of the oceanic microbial community is viruses. These small particles, typically 0.02–0.3 μm long, are made up of genetic material

FIGURE 10.2   Natural community of bacterioplankton. *Source:* Colorized SEM image by R. M. Morris, courtesy of microscope.mbl.edu.

FIGURE 10.3   *Poterioochromonas* is a small chrysophyte alga that photosynthesizes but also engulfs bacteria. *Source:* Image by Bob Andersen and D. J. Patterson, courtesy of microscope.mbl.edu.

surrounded by a protein coat. They are not mobile and function only when they encounter and invade a suitable host and take over its cellular machinery. Virus numbers are about 10 times those of bacteria or 10^7/ml. Fuhrman (2000) points out that viruses infect bacteria, cyanobacteria, and protists and suggests that viruses are important agents of mortality for these organisms.

In the ocean, many of the phytoplankton are very small and must be considered a part of the microbial food web. Platt et al. (1983) estimated that 60–80% of oceanic primary productivity is carried out by phototrophs less than $1 - 3$ μm in size. Although these organisms are extremely small, they can make up a large fraction of the total phytoplankton biomass and primary productivity (Sherr and Sherr, 2000). One abundant form, coccoid cyanobacteria of the genus *Synechococcus*, are about 1 μm in diameter and are found in the euphotic zone (10^2–10^5/ml). Another abundant group, bacteria in the genus *Prochlorococcus* are about 0.7 μm in diameter (10^4 to $> 10^5$/ml; Li et al., 1992).

10.2.2 Dissolved Organic Matter (DOM)

DOM is very dilute in the pelagic ocean, ranging from 75 to 150 μmol C/l. It is composed of a complex mixture of compounds, most of which are refractory, that is, unavailable to bacteria, and remain in the sea for a very long time. Miller (2004) summarizes DOM dynamics by stating that although this material has radiocarbon ages of up to 6000 years, there are measurable annual cycles of concentration. It is likely that a fraction of the DOM, probably around 1%, or 0.75 to 1.5 μmol/l, is accessible by bacteria. Note that the biomass of bacteria is approximately 0.1 μmol C/l.
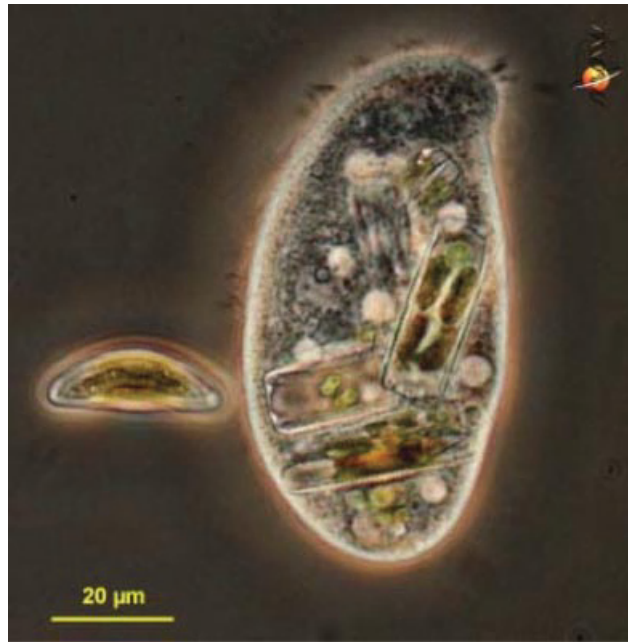
FIGURE 10.4 *Chilodonella* is a hypostome cililate with a mouth used to pick up bacteria and other particles. Here, the animal has ingested some small diatoms. *Source:* Image by Michele Bahr and D. J. Patterson, courtesy of microscope.mbl.edu.

10.2.3 Biomass and Productivity

It is characteristic of the oligotrophic ocean that biomass, calculated as C, is very similar for bacteria and phytoplankton (Table 10.1). The range shown, $1000-1500$ mg C/m^2 for bacteria in seven temperate and tropic ocean locations falls within the range of phytoplankton biomass ($447-4500$ mg C/m^2).

To investigate the dynamics of microbial food webs, however, productivity must be measured. For phytoplankton, the standard method is to incubate a sample in a bottle for a few hours with ^{14}C-bicarbonate, collect phytoplankton on a filter, and measure the ^{14}C incorporated by the phytoplankton. For bacteria, the procedure is similar except that samples are incubated with a radioisotope-labeled nucleic acid (thymidine) or an amino acid (leucine) that becomes incorporated into new DNA or protein.

For the sites in Table 10.1, the ranges of bacterial ($70-285$ mg C/m^2/day) and phytoplankton ($465-1548$ mg C/m^2/day) production are remarkably narrow. This is reflected in the ratio of bacterial to phytoplankton production ($0.09-0.26$). The reason this ratio is not closer to 1 is that bacterial production (BP) is a measure of the rate of synthesis of new bacterial biomass (also called *growth*) and not a measure of the total OM consumed by bacteria. To provide energy for biomass synthesis, and for general cell maintenance, some of the organic compounds the bacteria take up must be respired. The percentage of

TABLE 10.1 Bacteria and algae of the plankton at two sites in the Atlantic and at five tropic and temperate sites

Property	North Atlantic	Near Bermuda	Five Tropic and Temperate Sites
Euphotic zone depth (m)	50	140	74–175
Biomass (mg C/m^2)			
Bacteria	1000	1317	1142–1500
Phytoplankton	4500	573	447–1940
B : P	0.2	2.7	0.7–3.6
Production (mg C/m^2/day)			
Bacteria	275	70	56–285
Phytoplankton	1083	465	486–1548
B : P	0.25	0.18	0.09–0.26
Growth rates (per day)			
Bacteria	0.3	0.05	0.05–0.18
Phytoplankton	0.3	0.81	0.5–1.1
B : P	1	0.06	0.1–0.2

Source: Modified from Ducklow (2000).

organic carbon taken in by bacteria that is used for biomass is called the *growth efficiency* or the amount of new biomass produced per unit carbon consumed. In laboratory cultures, growth efficiency approaches 50%. In oceans, bacterial growth efficiency, measured by a variety of methods, ranges from 2% to 64% (del Giorgio and Cole, 2000). These authors conclude that

the lack of agreement about methods and the great range found indicates that the bacterial growth efficiency of oceans is not really known. Despite this, they argue that in natural marine waters, it is likely to be less than 30%. If a maximum value of 50% is used, then each day bacteria process 30–50% of the algal production. It follows that if a lower value is used for efficiency, then bacteria process even more of the algal production.

On the basis of the productivity data, it is obvious that the rates of activity in the microbial food web are strongly affected by the availability of nutrients. This is considered bottom-up control or control by the amount of the resource. In the ocean, productivity of algae and bacteria as well as the biomass of organisms and the grazing rate is higher in the coastal and upwelling regions than in the open ocean.

10.2.4 Grazers

Top-down control is also at work within the microbial food web as evidenced by the constancy of bacterial numbers from day to day or month to month. This occurs despite the fact that productivity of bacteria in the ocean is much more variable and approximates the productivity of photosynthetic algae. It is very likely that grazing by flagellates has a major impact on the numbers of bacteria. In turn, predation by ciliates controls the numbers of flagellates.

Flagellate abundance is approximately 1% that of bacteria. In the example in Table 10.2, they number 0.5×10^3/ml. Because of the size difference, however, the wet weight and the amount of carbon in flagellates are on the same scale as the carbon in bacteria.

In the laboratory, when small microcosms are set up with bacteria, flagellates, and ciliates, the populations oscillate in classic predator–prey relationships. The same changes likely take place in the open ocean, but it is very difficult to sample because exactly the

same water mass must be measured several times a day for weeks to find the cycles. There is at least one site, Limfjord, a shallow marine bay in Denmark (Fig. 10.5), where the cycles of bacteria, flagellates, and ciliates are in synchrony for weeks. In this system, bacteria ranged from 2.4 to 14×10^6/ml, flagellates from 200 to 17,000/ml, and ciliates from 1.5 to 160/ml. Each bacteria peak was followed by a flagellate peak 3–7 days later. Each flagellate peak was followed by a ciliate peak within 4–6 days. The ciliate cycle is not shown here. These data are strong evidence for the control of bacteria abundance by the grazing of microflagellates. They also indicate that flagellates, too, are likely controlled by grazing by ciliates (Lynch and Hobbie, 1988).

There is no well-accepted method for measuring the rates of bacterivory (Montagnes et al., 2008). One review states ''Bacterivory has proven to be one of the more intractable processes to measure'' (Strom, 2000, p. 358). One method uses the addition of tracer particles and measures the rate at which these particles are taken into the cells of grazers. Another method uses manipulations of the community, such as dilution, to change the rate of bacterivory and then looks at growth rate of the bacteria when grazing is reduced. Because of problems with these methods, most of the successful measurements have been made in coastal and estuarine habitats where bacterial productivity and the associated grazing rates are high compared with the oligotrophic ocean. For example, in Figure 10.6, only the rates in the small box are for the oligotrophic end of the productivity spectrum. In low productivity systems, BP is balanced by viral lysis and bacterivory (Strom, 2000; Breitbart et al., 2008; Jürgens and Massana, 2008). In other words, the viruses and bacterivores consume all the available bacterial productivity and in this way control abundance (top-down control).

It should be not be overlooked that in oligotrophic regions of the ocean where photosynthesis is dominated by bacteria such as *Synechococcus* and *Prochlorococcus*, the bacterivores also consume much of the primary productivity.

Viruses are considered a form of grazers in microbial food webs. Miller (2004) points out that the key measurements of the impact of viruses on bacteria in the ocean have been carried out in coastal waters. Methods for measuring this impact are imperfect (Helton et al., 2005), but estimates suggest that viruses are responsible for 20–40% of the total bacterial mortality and are similar in importance to grazing by protists (Suttle, 2007). Viral lysis of infected cells releases particulate and DOM, shunting that material

TABLE 10.2 Abundance and wet weight of the photosynthetic organisms, bacteria, and flagellates in the open ocean of the North Atlantic

Organism	Cells ($\times 10^9$/l)	Wet Weight (μg/l)
Picoplankton (0.2–2 μm)		
Cyanobacteria	12	1
Bacteria	600	20
Nanoplankton (2–20 μm)		
Photosynthetic algae	0.5	14
Flagellates	0.5	14
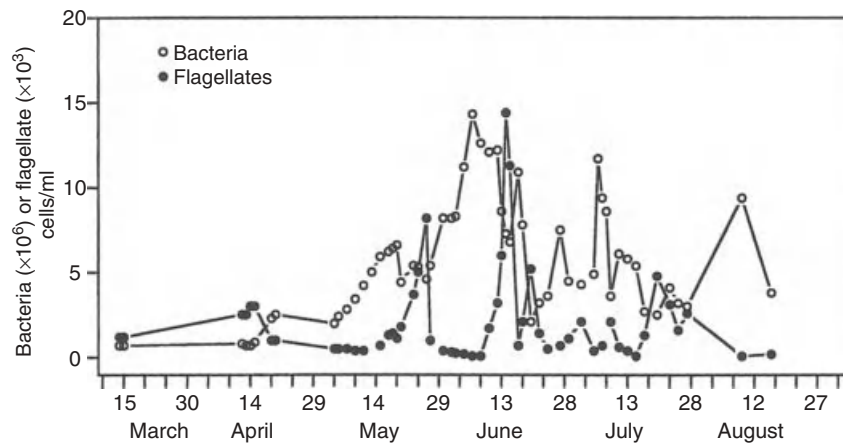
FIGURE 10.5 Bacteria and microflagllates (mean concentrations at 1 and 2 m) in Limfjord, Denmark. *Source:* Andersen and Sorensen (1986), redrawn in Strom (2000).
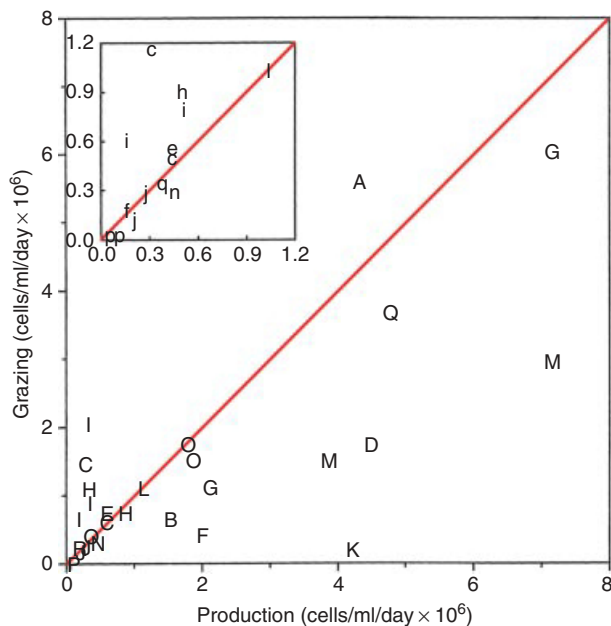
FIGURE 10.6 Bacterial production and grazing rates throughout the ocean. *Source:* Summary by Strom (2000).

away from grazers and toward heterotrophic bacteria (Suttle, 2005).

Mortality in ocean microbial food webs due to protist grazers and viruses generally keeps pace with production and growth, resulting in rapid turnover of microbial communities on the scale of days. This allows rapid reshaping of the species composition of these communities in response to any factor that influences the relative rates of growth or mortality of individual populations such as changes in resources, grazer prey selection, or grazer avoidance abilities (Strom, 2008).

10.3 ELEVATED PRIMARY PRODUCTIVITY

In the open ocean, inorganic nutrient limitation is the standard condition for planktonic communities, but in estuaries, these limitations are often relieved by terrestrial (and anthropogenic) inputs of nitrogen and phosphorous as well as silica, iron, and other micronutrients. This enrichment elevates phytoplankton productivity well above typical open ocean rates and causes more frequent bloom events (Chapter 4). OM produced by phytoplankton, together with allochthonous OM (discussed in the following section), fuels the microbial food web by stimulating production by bacteria (Table 10.3) and protists (Landry and Calbet, 2004). The result is a more abundant and more active microbial food web. However, several other changes at organismal and ecosystem scales, such as shifts in phytoplankton cell size, bacterial growth efficiency, and eutrophication, cause nonlinear changes in microbial food web activities and alters their relative importance to the planktonic ecosystem.

10.3.1 Phytoplankton Cell Size

Primary production (PP) in oligotrophic tropical and subtropical waters is accomplished mainly by picophytoplankton (<2 μm in diameter or length) such as *Synechococcus* and *Prochlorococcus* spp., and nanophytoplankton (2–20 um), which are mainly autotrophic and mixotrophic flagellates (Malone, 1980; Platt et al., 1983). Organisms in these size classes can be grazed directly by heterotrophic

TABLE 10.3 Bacterial abundance and production rates in some marine ecosystems

Regime	Abundance ($\times 10^9$ cells/l)	Production (mg C/m^3/day)
Estuaries	1–25	40–130
Salt marshes	5	100
Coastal ocean	0.5–3	5–120
Open sea	0.1–2	10

flagellates and ciliates. In fact, one study suggests that small phytoplankton are preferentially grazed over heterotrophic bacteria by a factor of 6–7 (Landry and Calbet, 2004). In these systems, almost every bit of newly produced OM feeds into the microbial food web either directly through grazing or indirectly via bacteria uptake of exuded DOM.

In estuaries, the size of individual species in phytoplankton communities becomes larger (Iriarte and Purdie, 1994; Sin et al., 2000). With some notable exceptions (Jochem, 1989; Phlips et al., 1999; Murrel and Lores, 2004), eutrophic estuaries are dominated by nanophytoplankton and microphytoplankton (>20 µm; e.g., diatoms and large dinoflagellates). This shift means that a lower percentage of phytoplankton biomass can be directly grazed by protists (Fig. 10.1), and instead, this biomass is consumed by larger metazoan grazers (Thingstad and Rassoulzadegan, 1999). One meta-analysis of nearly 800 independent measurements of protist grazing rates lends support to this conclusion (Table 10.4), although the degree to which the protist's share in PP is reduced from open ocean to estuaries remains somewhat uncertain (Landry and Calbet, 2004). One consequence of the shift away from picophytoplankton is that the portion of production by large phytoplankton that enters the microbial food web is restricted to DOM. This material is exuded from living phytoplankton cells, released from the front end (''sloppy feeding'') and

TABLE 10.4 Comparisons of percent primary production grazed per day by protists based on a synthesis of results from paired measurements ($n = 392$) of autotrophic growth and grazing mortality rates

Habitat	% Consumed
Estuaries	38.6 ± 2.5
Coastal ocean	56.6 ± 2.9
Open ocean	78.0 ± 1.8

Source: Data are averages (±standard errors) for oceanic, coastal, and estuarine habitats. Modified from Calbet and Landry (2004).

back end (excretion) of animal grazers, and produced during the decomposition of ungrazed cells. Thus, as phytoplankton cell size increases, the percentage of phytoplankton biomass directly supporting the microbial food web decreases and protist grazers must rely more heavily on heterotrophic bacteria as a food source.

10.3.2 Bacterial Growth Efficiency

The growth efficiency of bacteria, or the amount of new biomass produced per unit organic carbon consumed, increases systematically with the rate of BP and the trophic complexity of the ecosystem (Robinson, 2008). According to del Giorgio and Cole (1998), the differences in growth efficiency are rather extreme; efficiencies in oligotrophic open ocean water can be less than 0.01, while efficiencies in eutrophic environments can be greater than 0.5 (Fig. 10.7). This means that bacteria in resource-rich environments such as estuaries can channel a greater percentage of the OM they consume toward new biomass. Explanations for this trend remain unclear and may involve regulation by temperature, salinity, nutrient supply, and OM. However, analyses of bacteria in culture demonstrate that the availability of stoichiometrically balanced nutrition, which we might expect to find in resource-rich environments, allow bacteria to grow more efficiently (Russell and Cook, 1995).

The implications of this trend for the microbial food web are twofold. Higher growth efficiency means that more of the total carbon consumed by bacteria is used for anabolism (i.e., production or growth) and less is used for catabolism (energy production). Extra biomass production by efficiently growing bacteria supplements the already elevated BP in eutrophic estuaries and may make the microbial food web a more valuable link for transferring particulate and dissolved energy and materials to higher trophic levels. Conversely, efficiently growing bacteria exhibit relatively reduced rates of catabolism or mineralization of OM. In a relative sense, this diminishes the role of microbial food webs as recyclers of nutrients and OM. However, since growth efficiencies never greatly exceed 0.5, microbial food webs should always be considered important recyclers of OM.

10.3.3 Impacts of Eutrophication

Eutrophication, or the anthropogenic elevation of nutrient inputs to an ecosystem, can cause and maintain several large-scale alterations in the estuaries that have implications for microbial food webs. Eutrophied estuaries (and in a sense, all estuaries are eutrophied compared with the open ocean)

(a)

(b)

FIGURE 10.7 (a) Relationship between bacterial growth efficiency (BGE) and bacterial production using 237 paired measurements of bacterial production and respiration and (b) relationship between BGE and net phytoplankton production in which BGE was calculated from bacterial production using a model based on data in (a). *Source:* Figure after del Giorgio and Cole (1998). Used with permission.

experience a general shift in the type of organisms that dominate primary productivity from benthic microalgae and macrophytes to phytoplankton. This shift to the plankton enhances the activity of planktonic microbial food webs.

However, in many eutrophic estuaries, planktonic primary productivity is so high that the oxygen demand of remineralizing microbes exceeds the rate of reoxygenation, resulting in large areas of hypoxic (<2 mg O_2/l) and anoxic (0 mg O_2/l)

bottom waters. This condition occurs seasonally in many salt stratified estuaries such as the Chesapeake Bay, but it can be a permanent feature in fjords where anoxic deep water is retained in the system and is only rarely mixed with surface water. The effects of hypoxia/anoxia on large animals are universally negative. It kills benthic animals and restricts the habitat of pelagic animals, including many commercially important species (Officer et al., 1984). Regions of hypoxia/anoxia are commonly referred to as *dead zones*.

The effects of hypoxia/anoxia on the microbial food web are not as clear. Heterotrophic bacteria and protists are responsible for reducing oxygen levels in these waters, and they are generally abundant and grow well in hypoxic/anoxic waters (Fenchel et al. 1990, 1990; Bastviken and Tranvik 2001). So rather than being "dead zones," hypoxic/anoxic waters in estuaries are actually quite alive and are environments in which microbial food webs completely dominate biological activity.

Bacteria and protists in anoxic waters tend to be taxonomically different than those in oxic waters (Crump et al. 2007; Stock et al. 2009), and, theoretically, they have reduced growth efficiencies because they must use metabolisms that are less energetic than aerobic (oxygen-based) respiration. Experiments with cultivated bacteria and protists support this statement (Fenchel and Finlay 1990), although field observations of reduced growth efficiency in anoxic waters are mixed and are only available for freshwater systems (Cole and Pace 1995; Rossetti et al. 2001; Bastviken et al. 2003). The combination of reduced growth efficiency and the absence of metazoan grazers essentially eliminates the role of microbial food webs as links to higher trophic levels and magnifies their role as remineralizers of OM. This directly contrasts with the situation in oxic waters discussed earlier in which bacterioplankton have elevated growth efficiencies and may provide more nutrition to higher trophic levels.

A central unanswered question about eutrophied estuaries is: Why does not elevated primary productivity translate linearly into elevated productivity of harvestable organisms such as finfish and shellfish? Conventional wisdom states that the microbial food web consumes much of the excess phytoplankton production. Planktonic microbial food webs are more productive in eutrophic ecosystems, and they also benefit from nonlinear shifts on scales of organisms (elevated growth efficiency) and ecosystems (from benthic to planktonic production). But these benefits may be counteracted by a reduction in their share of phytoplankton production when larger

phytoplankton become abundant. Also, while the transfer of materials from microbial food webs to higher trophic levels is enhanced by higher growth efficiencies, it can be severely reduced in systems that develop hypoxia/anoxia. The balance between these competing factors remains to be defined, but if conventional wisdom proves to be true, nonlinear enhancements of microbial activities must dominate in eutrophied estuaries.

10.4 MULTIPLE SOURCES OF ORGANIC MATTER

In the ocean, bacterial metabolism is entirely dependent on photosynthesis and grazing processes that supply DOM through a great variety of mechanisms such as exudation, excretion, and sloppy feeding. As a result of this dependence, it is common to observe a close correlation between bacteria and phytoplankton properties such as abundance versus chlorophyll or BP versus PP (Cole et al., 1988). Such relationships are not usually seen in estuaries because there are multiple sources of OM besides phytoplankton for bacteria to use. These sources include OM from land as well as OM from fringing freshwater and salt marshes, sediments, and the coastal ocean. These external inputs of OM to planktonic microbial food webs provide potentially large subsidies for bacterial metabolism.

Terrigenous OM is often the largest external source of OM to estuarine microbial food webs. Estuaries typically receive runoff from watersheds with large surface area in comparison to the size of the estuary. For example, Chesapeake Bay (12,500 km^2) receives input from a watershed 179,000 km^2 in area, supplying $10-40\,gN/m^2$ of the Bay per year to fuel PP. OM inputs are proportionally large and may exceed the OM supply from photosynthesis *in situ*. With the enhanced supply of OM, BP rates may be an order of magnitude greater than that in the open ocean (Table 10.3), exceeding 100 mg C/m^3/day (Ducklow and Shiah 1993).

Another important source of OM to estuarine microbial food webs is aquatic plants. Most estuaries have fringing marshes, both freshwater and saltwater, and beds of submerged aquatic vegetation (SAV; see Chapters 5 and 6). Marsh plants and SAV may exude copious amounts of DOM in forms readily accessible to bacteria and also provide large inputs of particulate detritus during the period of senescence in the fall and winter.

10.4.1 Tracing Sources and Utilization

Biogeochemical processing by microbial food webs in estuaries influences the transport of externally supplied OM from land to the coastal ocean. Input and processing of this OM is frequently traced with stable isotopic signatures, carbon-to-nitrogen ratios, molecular tracers such as lignin phenols or lipids, and more recently with fluorescence excitation/emission analysis and with electrospray ionization coupled to Fourier transform mass spectrometry. OM in estuaries is a very complex mixture of compounds, most of which have not been identified. Simply following changes in bulk DOC concentration often gives a misleading picture of its turnover because of continual decomposition and addition from phytoplankton, seagrasses, and adjoining marshes and mangroves. Molecular analysis of DOC composition shows that different compounds are metabolized or removed at different rates and with different efficiencies (Benner and Opsahl 2001). Studies employing several chemical techniques, including fatty acid biomarkers, fluorescence spectra (Stedmon and Markager 2005; Fellman et al. 2011), and mass spectrometry (Sleighter and Hatcher 2008), suggest that a substantial terrigenous signature persists in the dissolved phase along the estuarine salinity gradient. In contrast, seaward-flowing particulate OM is dominated by a mixed phytoplankton/zooplankton signature with only nominal terrestrial influence (McCallister et al. 2004).

The most practical tool for tracing the sources and identity of OM flowing into and through estuaries is isotopic analysis. As seen in Table 10.5, stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) have different isotopic signatures in different sources (e.g., terrestrial vegetation, soil humus, fresh and marine plankton, and marsh grasses). Therefore, bulk OM in any given area or time, which is often a mixture of those sources, will have an isotopic signature reflecting the relative importance of the different sources. The signatures for a single element may overlap for different sources (e.g., ^{13}C in terrestrial OM and freshwater phytoplankton), so using more than one tracer helps distinguish among sources. From the data in Table 10.5, it appears that riverine DOM is likely to come from soil or terrestrial plants rather than from phytoplankton. An additional insight comes from the radiocarbon (^{14}C) in these samples. Positive values of δ^{14}C indicate OM less than 50 years old as a result of the large spike of ^{14}C added to the atmosphere by the bomb tests in the 1950s. The radiocarbon data indicate that the riverine DOM in the York River comes mostly from soil OM rather than from phytoplankton. While

TABLE 10.5 Stable isotopic and radiocarbon signatures for organic matter sources in estuaries

Source	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\Delta^{14}C$ (‰)
Terrestrial plants	−26 to −30	−2 to +2	—
Terrigenous soil	−23 to −27	2 to 6	152 to 310
Freshwater phytoplankton	−24 to −35	5 to 8	110 to 164[a]; −44 to −74[b]
Estuarine phytoplankton	−18 to −24	6 to 9	47 to 72
Salt marsh plants (C-4)	−12 to −14	3 to 7	—
Freshwater marsh plants (C-3)	−23 to −26	4 to 6	45 to 58
Benthic algae	−12 to −18	0 to 5	—
Estuarine DOM	−24	—	−77
Riverine DOM (high molecular weight)	−27 to −28	4 to 5	434[a]; −73 to −137[b]

[a] York River, VA.
[b] Hudson River, NY.
Source: Modified from McCallister et al. (2004).

most river systems are similar to the York River, the negative values for freshwater phytoplankton and DOM from the Hudson River tell us that the Hudson system has an additional, unusual, source of carbon. It is likely that the negative values are caused by carbon from a source of very old carbon in the watershed.

It is relatively straightforward to characterize OM in estuaries, assuming that different fractions can be separated for analysis. Making the connection between specific sources and their use by bacteria is more complicated. Coffin et al. (1990) grew bacteria in filtered estuarine water and then extracted bacterial DNA for stable carbon isotopic analysis. They showed that bacteria grown in water from Plum Island Sound, Massachusetts, were isotopically similar to *Spartina* or upland plant material. In a more comprehensive study, McCallister et al. (2004) determined the multiple isotopic content ($\delta^{13}C$, $\delta^{15}N$, and

$\Delta^{14}C$) of bacteria biomass collected in the estuaries of the York River, Virginia, and the Hudson River, New York, in different locations and seasons (Fig. 10.8). The position of bacteria samples on the dual isotope plot explains the specific mixture of OM sources used to synthesize biomass. In the examples shown for the York River, bacteria in the midsalinity reach of the estuary on average over the year used OM composed of 9% riverine terrigenous DOC, 56% estuarine (*in situ*) phytoplankton, and 35% marsh-derived OM. In other words, bacteria derived about half their carbon from phytoplankton-based sources and half from externally supplied OM.

10.4.2 Consequences for Bacteria

External sources of OM elevate estuarine BP over oceanic production by increasing the food supply.
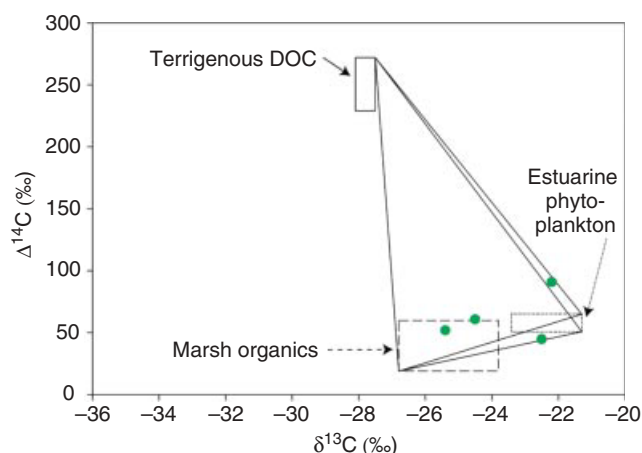
FIGURE 10.8 Isotopic signatures of bacterial biomass in the York River, VA. The closed circles show bacterial biomass collected in the midsalinity reach of the estuary. The boxes represent terrigenous DOC (solid line), marsh organic matter (dashed line), and local (estuarine) phytoplankton (dotted line). The triangle encompasses all possible compositions of bacterial biomass. Symbol positions suggest bacteria are mostly supported by phytoplankton and marsh-derived material.

Earlier we observed that oceanic BP was about 10–15% of the PP and that their growth efficiencies were 15–30%. If the ratio of BP to PP is 0.15 and the bacteria are using the PP with 10% efficiency, the total amount of carbon they are consuming is 150% of the PP (i.e., $0.15/0.10 = 1.5$). This scenario is possible for brief periods, for example, when a large phytoplankton bloom is decomposing, but is impossible to sustain for an extended duration. In estuaries, this situation is not uncommon because local PP is always subsidized with OM from bordering ecosystems. BP in mesohaline Chesapeake Bay averaged 22% of the local PP. Assuming a bacterial growth efficiency of 15% (it may be lower for marsh- and river-derived OM and higher for OM of phytoplankton origin), the amount of OM used by bacteria for respiration plus growth is 0.22/0.15 or 150% of the local production. A more detailed look is possible for the York River, where bacterial and phytoplankton rates have been studied intensively. At the freshwater, midestuary, and river mouth stations, annual bacterial productivity averaged 150%, 20%, and 8% of the local phytoplankton production. In the narrow, upper reaches of the estuary receiving the largest amounts of terrigenous material and adjacent to fringing marshes, the bacteria must consume much greater amounts of OM than are produced within the water column. In contrast, in the high salinity mouth of the estuary, the phytoplankton–bacteria interaction is similar to an oceanic type system. Raymond et al. (2000) observed that the York River released CO_2 to the atmosphere during much of the year and was a net heterotrophic system, consuming more OM than it produced internally. This is consistent with high bacterial metabolism in the system and is a common feature of estuaries generally (Caffrey, 2004).

Although the importance of OM from outside sources is probably very common in estuaries, there has been just one comprehensive study examining the sources for bacterial metabolism that attempted to identify the full range of subsidies available and compare bacterial and other aspects of system metabolism (Larsson and Hagström, 1982). There are only a few studies that measured BP and PP over the same periods, time, and space scales to facilitate comparison. One of the best remains an early study in the Baltic Sea where BP:PP ranged from 18% to 24% (Larsson and Hagström, 1982). However, the approach in this study was limited to that part of the BP supported by simultaneous photosynthesis, without considering other OM sources. Total BP:PP in the coastal Baltic may have been larger than reported in that paper. There are also many estuaries where more fragmentary information suggests low BP:PP ($\leq$10%) and the

net metabolism is autotrophic. As yet we have little basis for understanding or predicting the sign of net metabolism, that is, positive or negative, in any particular estuarine system.

10.5 EXTENDED WATER RESIDENCE TIME

Plankton organisms without specific means of staying within the estuarine system can only persist and grow if their growth rate exceeds the washout (flushing) rate of the estuary or if special circulation features concentrate and retain them (Hood et al., 1999). In its simplest form, this reflects the principle of the chemostat, which is an experimental system of microbes contained in a growth chamber that is continually fed fresh nutrients at one end while continually draining liquid at the other. However, chemostats are poor models of estuaries because they are very well mixed and only have one single source for one limiting nutrient. Estuaries are not so well mixed and estuarine circulation provides several mechanisms for extending the retention time (the inverse of the washout rate), potentially allowing organisms to persist and accumulate. In addition, as we saw above, bacteria in estuaries may have multiple sources of OM and nutrients and different reaches of an estuary may be limited by different factors. This produces a mosaic of conditions and communities, each with distinct relationships between growth and flushing rates.

Pritchard (1955) classified estuaries based on circulation and stratification: highly stratified, partially mixed, and well mixed (Chapter 2). These estuarine types differ in patterns of circulation, mixing, and, most importantly, flushing and retention times. These latter phenomena affect the dynamics of populations growing in different regions of estuaries.

The flushing or dilution rate of an estuary can be approximated using the simple equation:

$$D = \frac{Q_f}{V_f} = \frac{Q_f S_B}{V[S_B - S_0]} \tag{10.1}$$

where Q_f is the freshwater input rate and V_f the freshwater volume, which is approximately equal to

$$V \frac{S_B - S_0}{S_B} \tag{10.2}$$

where V is the total estuarine volume, S_B the end member salinity (e.g., the ocean), and S_0 the average salinity of the estuary, or subestuary, under consideration. For stratified systems, S_B is the salinity of bottom water and S_0 is that of the surface water.

In this equation, D, the dilution rate (per day), is directly proportional to the freshwater input rate (Q_f, m^3/day) and the bottom water salinity (S_B, dimensionless) and inversely proportional to the volume of the estuary (or part of it, V, m^3) and the surface–bottom salt difference ($S_B - S_O$; Ketchum et al., 1951). Using this formula, it is easy to see that increasing the freshwater input increases the dilution (flushing) rate and increasing the salinity gradient decreases the dilution rate. That is, more stratified estuaries have lower dilution rates and are better at retaining bacteria.

Plankton can only be retained in estuaries according to this mechanism if the dilution rate approximates the growth rate of the organisms. Bacterial growth rates in natural waters are in the order of 0.1–1/day. The dilution rates are similar. For example, in the mesohaline region of Chesapeake Bay, Q_f was $1–20 \times 10^7$ m^3/day, V was 5×10^9 m^3, and $[S_B - S_0]$ was approximately 5 for $S_B = 16–22$. Thus, D ranged from 0.02 to 0.07/day, well below bacterial specific growth rates (Malone et al., 1988). It is not surprising that bacterial abundance in the mid-Chesapeake Bay typically reaches greater than 5×10^9 cells/l in summer when growth rates are high. In winter, when growth rates are lower, the abundance falls to $\leq 1 \times 10^9$ cells/l. In the smaller, well-mixed Parker River estuary ($V = 10^6$ m^3; $Q_f = 10^5$ m^3/day), flushing rates in the midestuary were 0.05–0.25/day (Vallino and Hopkinson, 1998). These authors also used a more complex, realistic way to estimate the flushing rates. The important point of this analysis is that the physical dimensions and circulation processes in estuaries have characteristic timescales that match the timescales of biological processes such as growth rate. Physical and biological processes can interact strongly in these systems.

Another important consideration is that the absolute growth rate per se is not the important quantity for determining the balance between dilution and growth. Rather, the net growth rate is the critical process. The net growth rate is the difference between the specific growth rate and the sum of the rates of removal of bacterial cells by predation and viral mortality, plus other minor processes such as export on sinking particles. Predation by microflagellates and possibly viral lysis can be important mechanisms of bacterial mortality and tend to be closely coupled with variations in bacterial abundance and growth. Therefore, removal rates are likely to be quite similar to the specific growth rates, and the net growth rates are likely to be small—close to the dilution rates estimated above. Finally, remember that even very low net accumulation rates lead rapidly to large accumulations. A net rate of just 0.1/day leads to a doubling of the stock in 7 days and tripling in 11.

This approach can be elaborated by dividing an estuary into a series of compartments or sections and computing the dispersion rates and flushing times for each section. Then the bacterial abundance in each segment can be measured, and by combining these data with measurements of salinity, the net fluxes of bacteria (or any other property) can be calculated with a family of equations describing the dynamics of each box. This approach was first applied to the upper St. Lawrence River, a partially mixed estuary with energetic tides and a large freshwater input (Painchaud et al., 1996). The schematic diagram shows that the estuary is divided into upper and lower layers and into a series of upstream–downstream segments. In the example shown (August, 1987; Fig. 10.9a), the fluxes were large at the freshwater end, indicating that the river was an important source of bacteria flowing into the estuary. The net fluxes integrate all the physical and biological source and removal processes; and they were negative in all reaches, indicating the importance of removal processes (predation and viral lysis). For example, in surface box 3, 69×10^{18} bacteria/h flowed in from upstream, while 4×10^{18} were added from the lower layer and 47×10^{18} flowed downstream. The net flux ($69 + 4 - 47 = 26$) must be balanced by a net internal biological loss, to keep the bacterial abundance relatively constant over time (supported by observations). Otherwise, the bacterial abundance would be expected to increase steadily over time in the box. Independent measurements of growth and removal showed that these processes tended to be closely balanced most of the time. Normalizing these fluxes to the volume of each box gives the net fluxes in cells/l/h (Fig. 10.9b) and shows that the net fluxes are really quite low (for surface box 3, -12×10^6 cells/l/h, for an abundance of 10^9 cells/l). In this example, the residence times in the boxes were short, 11–24 h, indicating the bacterial dynamics were dominated by physical circulation.

A final example illustrates the interplay between circulation and OM fluxes in the York River estuary (Schultz et al., 2003). In contrast to the St. Lawrence, the river was not an important source of bacteria to the York River, VA. Bacterial abundance was lowest at the freshwater end in all months over a 2-year sampling period (Fig. 10.10). Abundance was high at the mouth and the abundances were strongly correlated with salinity, suggesting that bacterial abundance at any point along the salinity gradient is just the result of conservative mixing between the two end members. This view is simplistic and inaccurate. BP, represented here by the rate of thymidine incorporation, showed
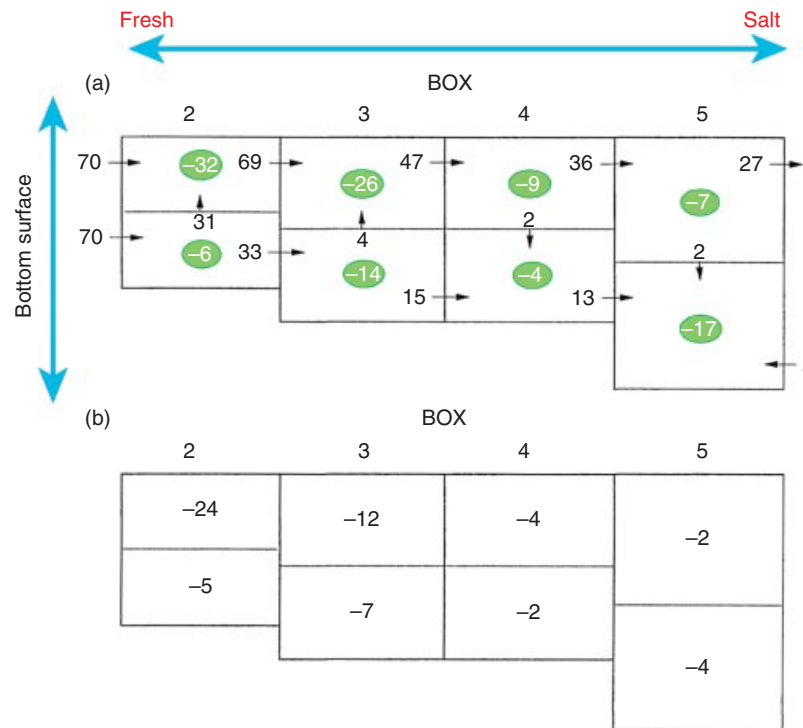
FIGURE 10.9 (a) Bacterial fluxes (10^{18} bacterial cells per hour) in the estuary of the St. Lawrence River, Canada. The numbers in the circles indicate the internal growth (+) or removal (−) rate from predators and viruses that balances the changes from physical transport. (b) Volume-normalized net fluxes (10^6 cells/l/h). *Source:* Figure after Painchaud et al. (1996). Copyright 2000 by the American Society of Limnology and Oceanography, Inc. Used with permission.

a significant but opposite correlation—it was highest at the freshwater end and declined toward the mouth. Bacterial growth rates (production divided by abundance) were very high at the freshwater end and much lower at the mouth. These growth rates might reflect the importance of external OM sources supplied in the freshwater input as discussed in the previous section. The pattern of rapid growth increasing upstream indicates that the upstream segments are in fact sources of bacteria as the water flows seaward. Here too, growth and removal are finally balanced and the net growth rates plus flushing interact to produce the smooth gradient in abundance that is observed along the estuary.

The interplay between biological (OM sources, growth, and removal) and circulation processes can best be represented in full-scale, time-dependent model simulations of estuarine processes (Xu and Hood, 2006). Unfortunately, few models include representations of bacteria. If they do, they tend to be crudely parameterized (Cerco, 1995; Hood et al., 2006). Now that OM inputs and bacterial growth in estuaries are better understood, perhaps bacteria can be modeled and the models used to frame testable

hypotheses about estuarine bacterial ecology (e.g., Keller and Hood, 2011).

10.6 METAZOAN GRAZERS

Estuaries are populated with many different metazoan grazers that consume members of the microbial food web. Some of these organisms, such as copepods, are also found in the open ocean, and graze on protists, but estuaries also host a broad array of benthic and surface-associated organisms.

10.6.1 Pelagic Grazers

Copepods (Crustacea, Copepoda) and euphausiids (Crustacea, Euphausiacea) are generally thought to be the most important pelagic suspension feeders in marine systems. Copepods are common in estuaries, including many euryhaline species, while euphausiids are truly marine organisms that are only occasionally found in the polyhaline reaches of estuaries (Simard and Lavoie, 1999). Adult copepods and euphausiids cannot graze free-living bacteria, but they often consume heterotrophic protists (Calbet
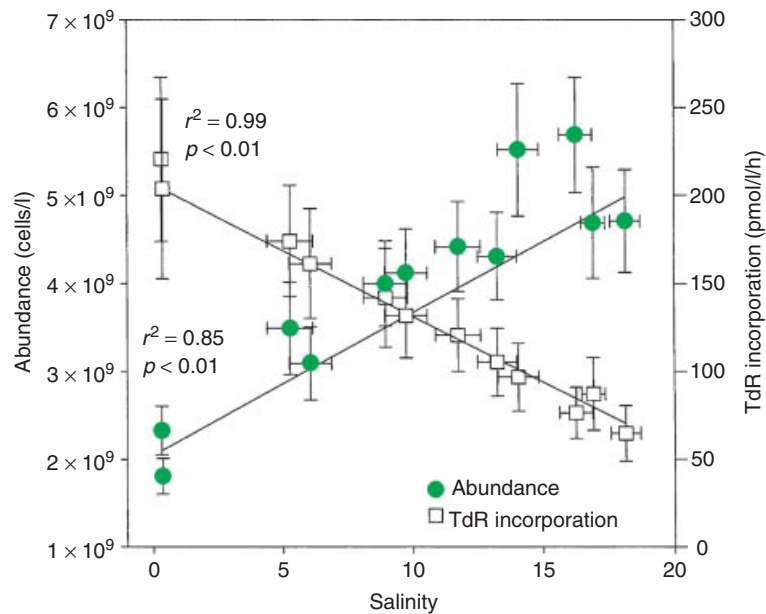
FIGURE 10.10 Bacterial abundance and thymidine incorporation rates (a proxy for growth) in the York River, VA. Samples were taken from the surface and bottom at six stations along the estuary during all months. The data represent the annual means for each property (including salinity) at each station along the estuary. *Source:* Figure after Schultz et al. (2003).
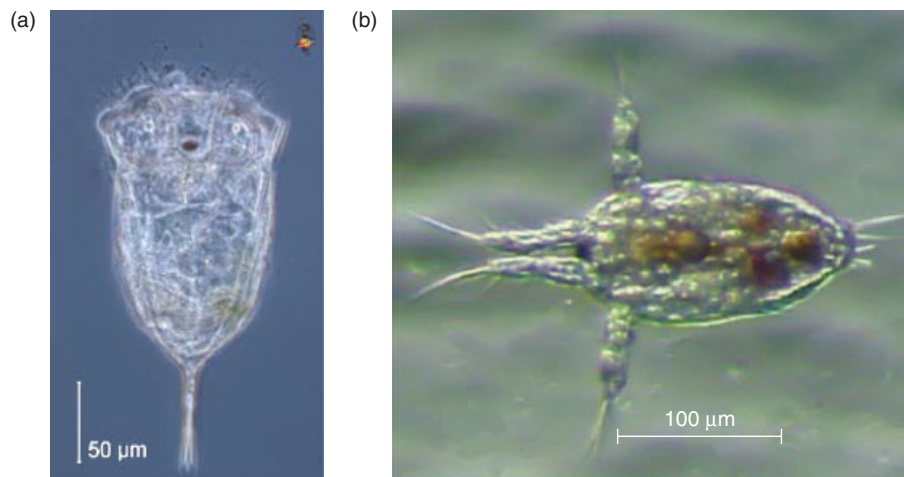
FIGURE 10.11 (a) *Keratella* sp., a rotifer common to estuaries that can ingest bacteria. They range in length from 90 to 150 μm. *Source:* Image by D. J. Patterson and Mark Farmer, courtesy of microscope.mbl.edu. (b) Nauplius larva of the calanoid copepod *Eurytemora affinis. Source:* Image by D. Devreker.

and Landry, 1999). Copepod nauplii (Fig. 10.11a) also consume protists and are capable of consuming bacteria-sized particles, though at a reduced efficiency (Roff et al., 1995; Turner, 2004). Filter-feeding rotifers (Fig. 10.11b), which are common freshwater suspension feeders, can also be very abundant in estuaries and are capable of consuming a wide range of particle sizes, including bacteria. However, the impact of nauplii and rotifer grazing on bacteria is minimal compared with that of protist grazers. Their influence on microbial food webs is mainly at the upper trophic levels where they have been shown to exert top-down control on the abundance of small ciliates and flagellates (Arndt, 1993; Uitto, 1996).

10.6.2 Benthic and Surface-Associated Grazers

The most obvious difference in the suspension-feeding community between estuaries and the

open ocean is the presence and, in some systems, the dominance of benthic and surface-associated suspension feeders. These include a wide range of organisms, including bivalves (such as clams, mussels, and oysters), barnacles, sea anemones, sponges, polychaete worms, and crustaceans. Of these organisms, the most ecologically important group influencing microbial food webs are bivalves because, like pelagic tunicates in the open ocean, they filter and remove organisms from large amounts of water. Perhaps the best example of the impact of bivalves on microbes is the invasion of zebra mussels (*Dreissena polymorpha*) to freshwaters in the United States (Ludyanskiy et al., 1993). Zebra mussels can filter particles ranging from 10 to 450 μm (i.e., ciliates, flagellates, rotifers, nauplii, and phytoplankton) and, like most bivalves, ingest or repackage them into rapidly sinking pseudofeces. These organisms are thought responsible for dramatic reductions in phytoplankton, heterotrophic protists, and, to some extent, turbidity in the Hudson River (Fig. 10.12) and other systems. Several groups have reported calculations of the filtering capacity of zebra mussels. For example, Roditi et al. (1996) calculated that zebra mussels, during their population peak in the 1990s, were capable of filtering a volume equivalent to the entire freshwater tidal portion of the Hudson River every 2 days.

Bivalves are often very abundant in estuaries and, in some cases, will effectively compete with planktonic suspension feeders (which they may also consume) for resources. In fact, in some estuaries, bivalves are capable of filtering all the water in the system in less than a day. Newell (1988) calculated that the historically (pre-1870) extensive oyster beds in Chesapeake Bay could filter the entire volume of the bay in a little over 3 days. He argued that, since then, the precipitous reduction in oysters from overharvesting allowed an increase in pelagic suspension feeders such as copepods and an expansion of the pelagic food web. The importance of bivalves in different estuarine ecosystems depends on abundance and species type as well as estuarine volume and water residence time. Dame (1996) expressed this impact as a ratio between clearance time and residence time (Table 10.6), such that bivalve grazing is more important in systems with low ratios (i.e., more rapid clearance rate and longer water residence time). Also, in a discussion of bivalve impacts on South San Francisco Bay, Cloern (1982) argued that water column stratification isolates surface water from benthic filter feeders, limiting their influence on the planktonic food web.

TABLE 10.6 A comparison of system clearance time by bivalve filter feeders to water volume residence time

System	Dominant Bivalves	Dominant Species	Volume ($\times 10^6$ m^3)	Biomass: Volume (g/m^3)	Clearance Time (Days)	Residence Time (Days)	Clearance: Residence Ratio
Asko	Mussels	*M. edulis*	4000	0.4	99	1.00E+05	0.01
S. San Francisco Bay	Clams, various	*P. amurensis*	2500	2.5	0.7	11.1	0.06
Oosterschelde	Mussels, Cockles	—	2740	3.1	3.7	40	0.09
Chesapeake Bay, Past	Oysters	*C. virginica*	27300	—	3.3	22	0.15
Bay of Brest	Clams, various	—	1480	7.4	2.8	16.7	0.17
Marennes-Oleron Bay	Oysters	*C. gigas*	675	4.2	2.7	7.1	0.38
Ria de Arosa	Mussels	*M. edulis*	4335	1.6	12.4	23	0.54
Western Wdden Sea	Mussels	—	4020	3.7	5.8	10	0.58
North Inlet	Oysters	*C. virginica*	22	15.4	0.7	1	0.70
Narragansett Bay	Clams	*M. mercenaria*	2385	—	25	27	0.93
Sylt, Eastern Wadden Sea	Mussels	*M. edulis*	7.2	21.7	2.1	0.5	4.20
Delaware Bay	Oysters	*C. virginica*	19420	—	1278	97	13.17
Chesapeake Bay, Present	Various	—	27300	—	325	22	14.17

Source: Adapted from Dame (1996).
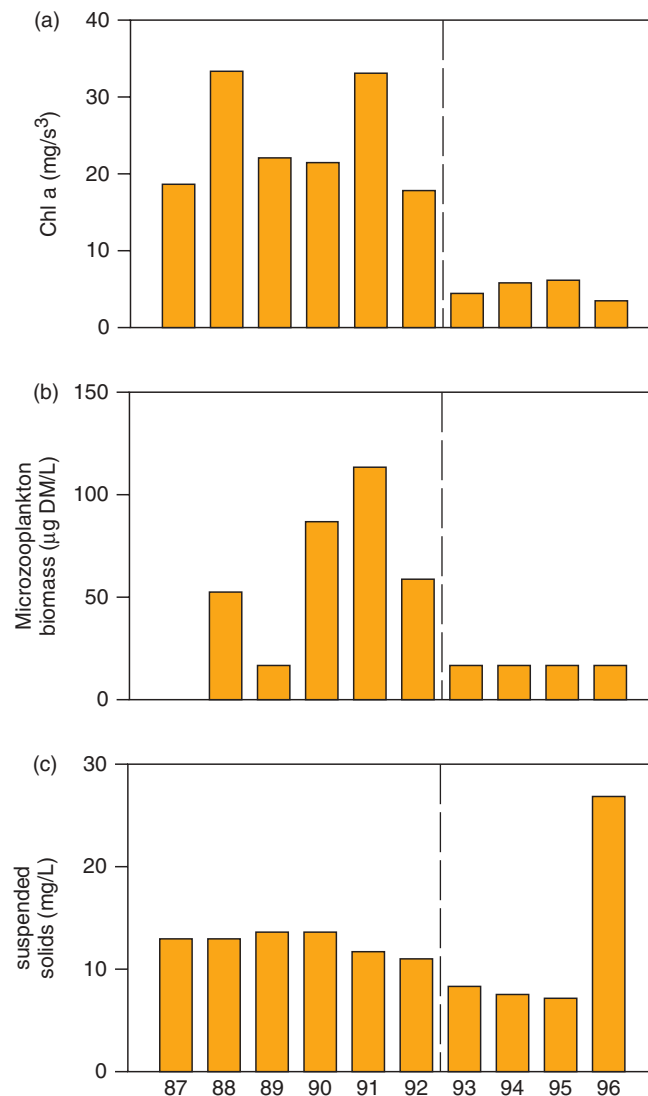
FIGURE 10.12 Changes in concentrations of edible and inedible particles in response to the arrival of zebra mussels in the Hudson River: (a) phytoplankton biomass from chlorophyll a, (b) microzooplankton biomass (tintinnids, rotifers, and copepod nauplii), and (c) suspended solids. The dashed lines show the point at which zebra mussels became abundant. Data are annual average means from Kingston, NY, during June–August. Zooplankton data are geometric means. Unusually heavy summer rains are responsible for the high suspended solids in 1996. *Source:* Figure after Strayer et al., 1999, copyright 1999, used with permission from the University of California Press.

The impact of bivalve grazing on microbial food webs depends on the particle size range they can efficiently filter. Most bivalves capture particles in the size range of heterotrophic protists, and several studies suggest that bivalve grazing can control populations of heterotrophic protists. Analyses of grazing by *D. polymorpha* (Findlay et al., 1998), *Crassostrea virginica* (Fig. 10.13), and *Crassostrea gigas* (Dupuy et al., 2000) in experimental systems showed that these bivalves greatly reduced the abundance of heterotrophic protists but did not reduce bacteria. In

the *D. polymorpha* study, bacterial abundance actually increased, suggesting that bivalve grazing reduced grazing pressure on bacteria by heterotrophic protists. Some bivalves can also filter free-living bacteria, including the mussels *Mytilus edulis* and *Geukensia demissa* and the clam *Potamocorbila amurensis*. One study showed a 30–35% reduction in bacterioplankton cells in tidal water passing over natural and experimental beds of *G. demissa* (Newell and Krambeck, 1995). Morphological analysis of

bacterioplankton in this study suggested that mussels preferentially removed larger bacterial cells.

In some estuaries, large volumes of water pass through stands of seagrass and other SAV, the leaves and shoots of which expand the effective benthic area by as much as 10-fold (Hemminga and Duarte, 2000). Most submerged plants host a complex epibiotic community composed of plants (epiphytes) and animals (epizoans), including suspension-feeding protists such as ciliates and suspension-feeding metazoans such as bryozoans, barnacles, and hydroids. This creates a gauntlet of suspension feeders that strip particles from the water column. Lemmens et al. (1996) estimated that epizoan suspension feeders associated with *Amphibolis antarctica* leaves could potentially filter daily the overlying water column. Experiments conducted by Agawin and Duarte (2002) suggest that seagrass canopies can trap as much as 70% of suspended particles in less than an hour. Much like oyster reefs and mussel beds, seagrass beds are sites of significant mortality for members of the microbial food web.

10.7 SUSPENDED PARTICLES

It seems clear that interaction with surfaces and surface-associated organisms distinguishes microbial food webs in estuaries from those in the open ocean. Perhaps the most extensive ''surface'' habitat in direct contact with plankton in both these systems is the surfaces of particles in suspension. These particles range in size from less than a micron in diameter (e.g., colloids) to several millimeters (e.g., marine snow). Particles large enough to provide habitat for microbes are usually aggregates of smaller particles and flocculated materials. The flocculated state of these particles would seem to complicate calculations of available particle surface area, but the self-similar structure of ''flocs'' simplifies the problem. On the basis of the relationships presented by Winterwerp and Van Kesteren (2004), it is possible to show that the surface area of typical flocs does not depend on the size of the flocs but is the same as if the particles were unflocculated (L. P. Sanford, personal communication). Calculations of the surface area of suspended particles indicate that in the ocean where suspended mass concentration is about 1 g/m^3, the surface area associated with particles is in the order of $1 \text{ m}^2/\text{m}^3$ of water (or per m). In coastal waters where suspended mass concentration is about 10 g/m^3, surface area is in the order of $10/\text{m}$. In turbid estuaries where suspended mass concentration is 100 g/m^3, surface area

is in the order of $100/\text{m}$. In all these examples, the surface area of suspended particles in the water column (surface area concentration multiplied by depth) far exceeds that of the underlying sediment surface and probably any other surface in direct contact with the planktonic environment.

Bacteria attached to suspended particles tend to be larger and faster growing than free-living bacteria, probably because of their proximity to particle-associated OM. As they grow, they form small biofilms by producing exopolysaccharide that they use to anchor themselves to the particles. These bacteria also produce a large amount of extracellular enzymes to degrade particulate organics to molecules small enough to transport across their cellular membranes. On the basis of the sequencing and analysis of cloned 16S rRNA genes, particle-attached bacteria and archaea in estuaries and the ocean are readily distinguishable from free-living organisms (Delong et al., 1993; Bidle and Fletcher, 1995; Crump et al., 1999; Kellogg and Deming, 2009).

Larger particles can develop an entire microbial food web of their own with surface-attached flagellates and ciliates feeding on attached bacteria. But particle-attached bacteria can also be consumed directly by metazoan grazers, such as copepods and rotifers. This short-circuits the microbial food web by passing materials and energy directly from detritus-consuming bacteria to higher trophic levels. Many estuaries have highly turbid regions where this is potentially an important pathway for nutrition. These regions, known as *estuarine turbidity maxima* (ETM), are highly productive zones that support dense communities of zooplankton and serve as spawning grounds for young anadromous fishes. They occur at the boundary between the landward intrusion of saltwater and the seaward flow of freshwater where riverborne particles are trapped and concentrated by estuarine hydrodynamics to levels as high as 1 kg/m^3. Bacteria attached to ETM particles can be extremely active and in some systems can dominate planktonic bacterial activity. For example, in the Columbia River ETM, Oregon, particle-attached bacteria are responsible for 70–90% of BP (Crump et al., 1998). Particle-attached bacteria are also very active in the ETM of the Chesapeake Bay but account for a lower fraction of total activity because free-living bacteria are also highly active (Griffith et al., 1994). Particle-attached bacteria in the open ocean are also very active but are much less abundant and have a reduced role in planktonic microbial food webs.

FIGURE 10.13 *Crassostrea virginica* reef in the Indian River Lagoon, Florida Bay, at low tide. *Source:* Photo by Kathleen Hill, courtesy of Smithsonian Marine Station at Ft. Pierce.

10.8 TEMPERATURE AND SALINITY

Temperature directly influences the growth rate of bacteria and other microbes, but its effects do not represent a strong contrast between estuarine and oceanic systems. Although estuaries may experience daily or short-term extremes in temperature variation, seasonal temperature ranges are similar to the open ocean. The greatest seasonal ranges in both estuaries and the ocean are in the temperate latitudes where the coastal ocean (e.g., New York Bight) ranges from about 2 to 25 °C. The Chesapeake Bay range is about 0–30 °C. Some tropical estuaries may experience higher temperatures, which push the microbial food web to its upper tolerance limits, but there are few observations of temperature effects in tropical estuaries or mangrove swamps.

Shiah et al. (1994) showed that bacteria in temperate estuaries have mesophilic responses to temperature throughout the year. That is, bacteria had about the same temperature optima for leucine and thymidine incorporation (around 25 °C) regardless of season and ambient temperature. More interesting was that at all times of the year, bacteria responded to temperature shifts in the same way. No matter what

the ambient temperature, the response curves (incorporation rate vs temperature) could be superimposed almost exactly.

Unlike temperature, salinity provides a strong contrast between estuaries and oceans. Salinity is a dominant gradient in estuaries, structuring the environment both physically (e.g., stratification) and biologically (e.g., species composition) and influencing microbial food webs in several different indirect ways described throughout this chapter. The direct effects of salinity on microbial food webs seem to be limited to the freshwater/mesohaline region of estuaries. Painchaud et al. (1987) showed mortality of freshwater bacteria with increasing salinity in the St. Lawrence. But increasing salinity also causes rupture of freshwater phytoplankton and protists, releasing DOM and making it available for bacteria. Several studies describe variations in bacterial properties along the salinity gradient in more detail. In one study on the York River estuary, assays of physiological capabilities at six stations along the entire estuarine gradient, and throughout the year (i.e., across the annual temperature range), showed that bacterial community composition separated into four assemblage types: cold, low salinity (<12 °C, <12 salinity); warm, low salinity (>21 °C, <12 salinity); cold, high

salinity; and warm, high salinity (Schultz and Duck-low, 2000). However, these observations could not be interpreted as direct effects of salinity but instead are probably controlled by factors that covary with salinity such as allochthonous inputs, circulation, and mixing. Crump et al. (2004) demonstrated that the phylogenetic composition of the bacterial community changed and adapted to intermediate salinity conditions in Plum Island Sound estuary, Massachusetts, but only in summer and fall when bacterial growth rate was relatively high and water residence time was relatively long. Thus, it is likely that estuaries support uniquely adapted communities of bacteria and possibly protists, but it remains unknown how differences in the species composition influences the form and activity of microbial food webs in estuaries.

10.9 CONCLUSIONS

Estuarine microbial food webs differ dramatically from the open ocean paradigm.

Eutrophication and elevated primary productivity in estuaries enhance microbial food web activity and also initiate several nonlinear changes such as increasing the average cell size of phytoplankton, elevating the growth efficiency of bacteria, and shifting primary productivity from benthic to pelagic.

OM from land and from aquatic plants supplements the nutrition of estuarine microbial food webs. Stable isotope and radioisotope composition studies confirm that estuarine microbial food webs consume and respire this OM.

Water residence time in estuaries is highly variable. Retention of planktonic microbes depends on the relationship between their rate of reproduction (growth) and their residence time in the estuary.

Metazoan grazers that consume members of microbial food webs in estuaries include benthic or surface-associated organisms that can be dominant locally or ecosystem-wide.

Particle-attached bacteria are more abundant in estuaries than in the open ocean and are often highly concentrated in ETM regions. Grazing on particles by metazoan grazers short-circuits the microbial food web by transferring material and energy directly from bacteria to higher trophic levels.

Isotope analysis of microbes holds promise for quantifying the relative importance of various food sources and for tracing the passage of these materials through estuarine food webs.

Ecosystem-level eutrophication studies in estuaries are revealing large-scale impacts that are intimately linked to microbial food web activities such as the formation of hypoxic bottom waters and a general shift from benthic to planktonic PP.

Invasions and introductions of bivalves and possibly other metazoans can affect microbial food webs directly through grazing on bacteria and protists and indirectly through consumption of phytoplankton and other food sources.

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ESTUARINE ZOOPLANKTON

Mark C. Benfield

11.1 INTRODUCTION

The term *plankton* is derived from the Greek word ''planktos,'' which means ''to drift or wander.'' Zooplankton are planktonic animals that cannot swim against moderate horizontal water currents. This definition is an oversimplification because within the zooplankton there are some taxa, or developmental stages within a particular taxon, that are incapable of swimming against all but the weakest currents, while others may be quite strong swimmers that are limited only by strong tidal flows. Zooplankton range from single-celled heterotrophic flagellates to complex metazoans such as copepods, mysids, ctenophores, chaetognaths, and cnidarians.

The waters of most estuaries teem with planktonic life. With a few exceptions, the combination of readily available nutrients, shallow depths that are illuminated by sunlight, and waters that are warmer than the coastal ocean produce conditions favorable for the growth of phytoplankton. In turn, these single-celled plants in combination with detrital material fuel a planktonic food web that produces abundant zooplankton.

11.2 ZOOPLANKTON CLASSIFICATION

11.2.1 Size Classification

Planktonic organisms are often classified according to their size. One widely accepted size classification system proposed by Sieburth et al. (1978) is illustrated in Figure 11.1. Most estuarine zooplankton occupy size ranges that span 20 μm to 2 cm (microzooplankton to mesozooplankton), although larger organisms such as ctenophores and cnidarians may also be abundant.

11.2.2 Ontogenetic Classification

Zooplankton that are planktonic for only a portion of their lives are termed *meroplanktonic*, while those that remain planktonic throughout their development are termed *holoplanktonic*. The transition from mero-plankton may occur when organisms develop more competent swimming capabilities and become nektonic, or when they settle out of the water column and metamorphose into benthic forms. A third group, called *tychoplankton*, contains benthic organisms that become transient members of the plankton when they are swept from the bottom by turbulence or currents.
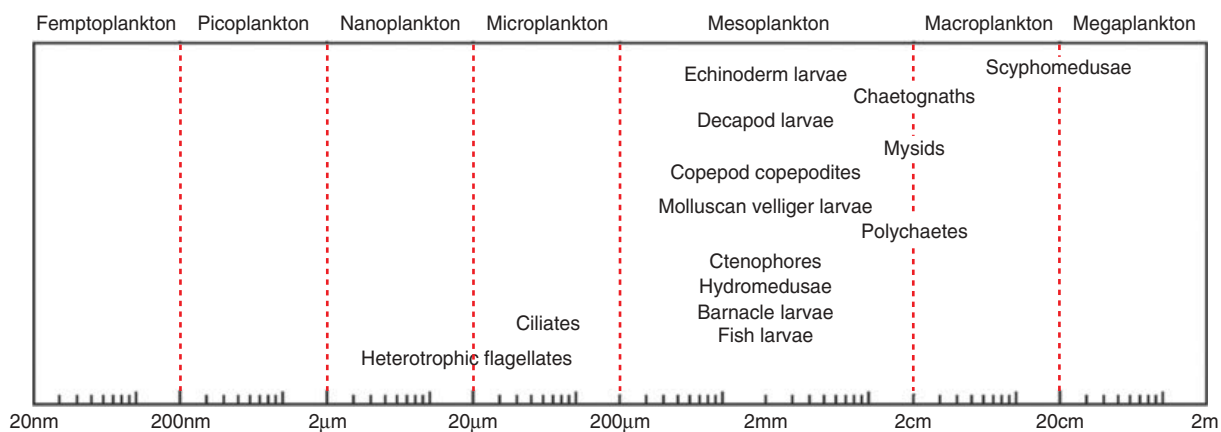
FIGURE 11.1 Size classification of plankton based on Sieburth et al. (1978). Note the logarithmic scale on the size axis. Most estuarine zooplankton range in size from ~2 μm (heterotrophic flagellates) to a maximum of ~1 m (large scyphomedusae).

Recall that the criterion for membership in the plankton is usually based on the swimming ability relative to directed horizontal currents. This distinction does not mean that all zooplankton are poor swimmers. Many have excellent swimming capabilities when moving vertically or with horizontal currents. Swimming capabilities usually improve as organisms grow in size. Consequently, small organisms are generally less competent swimmers than larger ones. For example, many zooplankton begin life as small larval forms with limited swimming abilities. As they grow, they become more capable swimmers and ultimately leave the realm of the plankton for that of the nekton. Many species of fish produce planktonic eggs and larvae that cease to be zooplankton when they become juveniles. Alternatively, many benthic or sessile organisms produce planktonic larvae. These meroplanktonic larvae cease to be plankton when they metamorphose into sessile or benthic ontogenetic stages. Examples of taxa with meroplanktonic larvae include oysters, barnacles, benthic ghost and mud shrimps, crabs, and penaeid shrimps.

11.3 DOMINANT ESTUARINE ZOOPLANKTON TAXA

Estuaries support high zooplankton biomasses that often exceed those found over the adjacent continental shelves. The species that comprise this high biomass vary according to the geographical location of the estuary, temperature, and the salinity regime within each system. Moreover, at any given time, the zooplankton assemblage in an estuary may contain a mix of marine, estuarine, and fresh water taxa, whose relative abundance depends upon factors such as distance from the sea, tidal stage, and hydrological conditions in the surrounding catchment.

Holoplanktonic mesozooplankton assemblages within estuaries are frequently dominated by copepods, cladocerans, and mysids. These small crustaceans have high secondary production and serve as prey for organisms in higher trophic levels such as fish, ctenophores, medusae, chaetognaths, and various decapod crustaceans. Meroplanktonic zooplankton usually include the larval forms of barnacles and other crustaceans, and mollusks.

Copepods are crustaceans that are the most abundant metazoans in the oceans. They also occur in high abundances in estuarine systems. Copepod development begins with eggs, which are either carried by the female or broadcast into the water depending upon the species. Eggs hatch and pass through a series of six naupliar and six copepodite stages with the final copepodite stage being the adult. The rapid generation times of copepods (20–30 days in subtemperate regions; Ianora, 1998) allow them to respond quickly to changing environmental conditions. Common estuarine copepods include species of the genera: *Acartia, Eurytemora*, and *Pseudodiaptomus*. In the lower reaches of estuaries, *Paracalanus* and the cyclopoid genus *Oithona* are often common. Species richness may be very high in tropical systems. For example, Revis (1988) documented 102 copepod species in a Kenyan estuary during an 11-month study, although only 12 species were dominant. Calanoid and cyclopoid copepods dominate the holoplanktonic zooplankton in most estuaries. They are important grazers of phytoplankton and microzooplankton and are, in turn, prey for zooplanktivorous fishes and invertebrates.

Mysids are small shrimplike crustaceans that often constitute a large fraction of the zooplankton numbers and biomasses in estuaries. Common estuarine genera include *Neomysis, Mysis, Mesopodopsis*, and *Rhopalophthalmus*. Mysids are among the larger estuarine zooplanktors. Their size means that in some cases they dominate the mesozooplankton biomass. For example, Wooldridge and Bailey (1982) reported that mysids exceeded 90% of the total mesozooplankton dry mass in the Sundays River estuary, South Africa. While mysids are generally regarded as omnivores (Mauchline, 1980), individual species are able to coexist in a single estuarine system by specializing on different prey and by varying their diets as prey abundances diminish. Their ability to switch prey as availability changes means that they can be important predators of a variety of different taxa including copepod nauplii and copepodites, rotifers, and other meroplanktonic larvae such as gastropod veligers (Winkler et al., 2007). They are important in the transfer of carbon from the microzooplankton, mesozooplankton, and detrital pools into small zooplanktivorous fishes and other larger invertebrate predators (Vilas et al., 2008).

Mysids play a key role in structuring estuarine food webs through their ability to select for different sizes of prey. Winkler et al. (2007) examined the feeding ecology of *Mysis stenolepis* and *Neomysis americana* in the St. Lawrence River estuary, Canada through a combination of controlled feeding experiments and stable isotope analyses. *Mysis stenolepis* was characterized as a raptorial feeder that selected for larger prey such as the copepodites of the copepod *Eurytemora affinis*. When its preferred prey were scarce, it switched to a filter-feeding mode and consumed more abundant smaller prey items such as copepod

nauplii, rotifers, and gastropod velligers. *Neomysis americana* was a filter feeder that opportunistically consumed the most available, and generally smaller, prey items.

Other invertebrates are also important constituents of estuarine holoplankton. Fresh water cladocerans such as *Bosmina* and *Daphnia* may be abundant at the fresh water end of the estuarine turbidity maximum (ETM). Toward the lower reaches of estuaries, cladocerans belonging to the genera *Podon* and *Evadne* may also be common. Gelatinous zooplankton such as ctenophores can be important predators of mesozooplankton. These predators primarily consume copepods, fish eggs, and fish larvae. The genera *Pleurobrachia* and *Beroe* are common in the middle regions of estuaries. The ctenophore *Mnemiopsis* and cnidarian scyphomedusae can reach high abundances in the middle and seaward ends of estuaries. *Mnemiopsis* is particularly tolerant of low salinities and the accidental introduction of *Mnemiopsis leidyi* into the Black Sea in the 1980s (Purcell et al., 2001) resulted in a population explosion that decimated anchovy populations until the accidental introduction of a predatory ctenophore *Beroe ovata* produced some biological control of *M. leidyi*.

11.4 PHYSIOLOGICAL CHALLENGES

Hydrographic properties in estuaries are generally regarded as being more variable than in the adjacent coastal ocean. This is a consequence of the dynamic nature of estuaries where tides, riverine discharge, and winds combine to mix and shift the spatial pattern of salinity, temperature, turbidity, dissolved oxygen, and other hydrological parameters that can affect the distributions of zooplankton. Many other chemical and biological factors such as food availability, predation, and pollutant concentrations display similar variability. The shallow depth of most estuaries compared to the coastal ocean makes estuaries subject to more frequent, higher amplitude temperature fluctuations than the coastal waters. In stratified estuaries, zooplankton that engage in regular vertical migration patterns experience substantial changes in their abiotic environment as they move through strong gradients in temperature, salinity, and potentially other factors (Laprise and Dodson, 1993). Estuarine zooplankton must therefore adapt to frequent physiological challenges driven by the continually changing nature of their milieu, or develop strategies that reduce the magnitude of these challenges.

Salinity is normally a key physical factor regulating the spatial distribution and structure of estuarine zooplankton. Most estuarine zooplankton are osmoconformers and each taxon has a range of salinities that are within its zone of physiological tolerance. Moreover, salinity may also influence the distributions of prey items (Kimmel and Roman, 2004), which will, in turn, affect the distribution of those organisms that depend on them for food.

Salinity zones within estuaries have typically been based on the Venice classification (Anonymous, 1959). This classification scheme divides estuaries into five salinity zones: limnetic (0–0.5 psu), oligohaline (0.5–5.0 psu), mesohaline (5–18 psu), polyhaline (18–30 psu), and euhaline (>30 psu). This scheme has been criticized as lacking biologically relevant boundaries by Bulger et al. (1993), who proposed a biologically based scheme consisting of overlapping zones derived from a statistical analysis of the zonation patterns of 316 estuarine species and life stages: 0–4 psu, 2–14 psu, 11–18 psu, 16–27 psu, and 24 psu to marine waters. Whatever system is employed, estuarine zooplankton frequently manifest definite horizontal zonations that vary with the prevailing tide and fresh water discharge.

Salinity fluctuates on short time scales associated with tidal cycles. In positive estuaries (those with salinity increasing toward the sea, see Chapter 2), the average salinity typically increases during floods and declines over ebbs. Moreover, the spatial distribution of isohalines is displaced inland by flood tides and seaward during ebbs. Estuarine zooplankton may engage in behavioral strategies designed to keep them within their physiologically preferred salinities. As an example of such behavior, the euryhaline estuarine copepod *E. affinis*, is evident in research by Devreker et al. (2008). In the Seine estuary, France, *Eurytemora affinis* is the numerically dominant copepod (90–99%) in the low salinity zone (0.5–15 psu) and it remains a dominant species in the zone for most of the year. Using very high resolution (15-min intervals over 50 h) sampling at the surface and bottom, Devreker et al. (2008) demonstrated how *E. affinis* maintains high abundances in the salinity zone it favors. Densities of adults and copepodids were higher near the bottom than in surface waters during ebbs (Fig. 11.2), suggesting a strategy to avoid being swept out of the estuary by ebb tides. Resuspension into surface waters occurs during early flood tides with consequent landward advection followed by active migration down into bottom waters during the latter part of the ebb (Fig. 11.2). In this manner, *E. affinis* is able to avoid being swept out of the
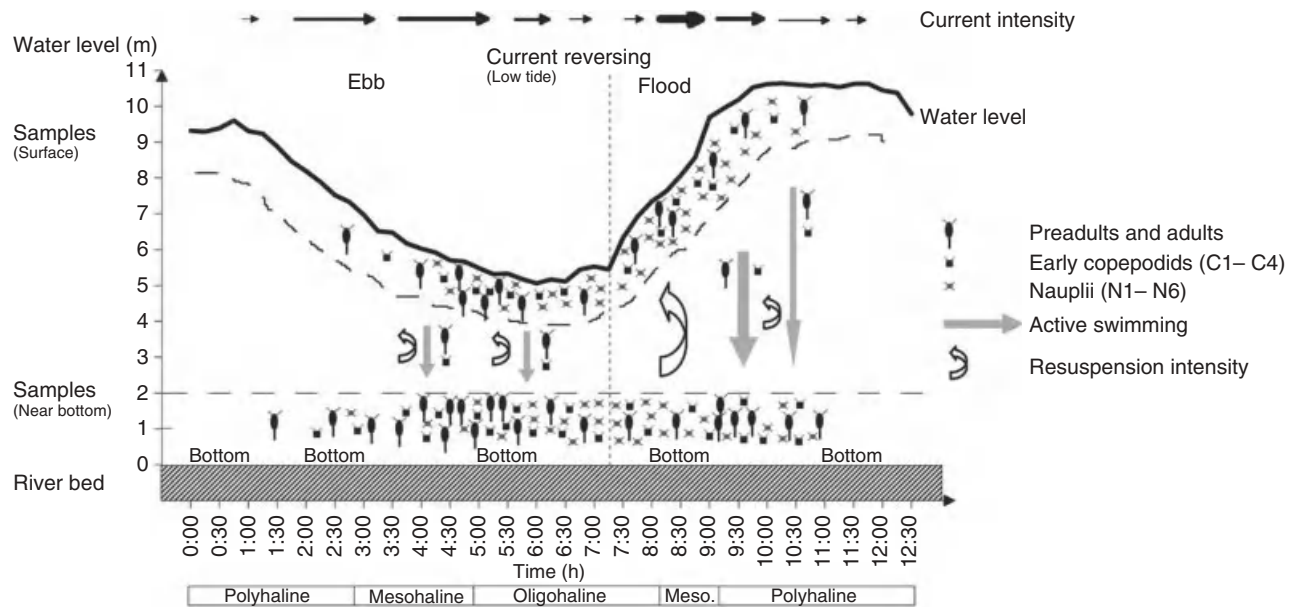
(1) According to the hypothesis of Morgan et al. (1997) and schmitt et al. (unpublished datd)

FIGURE 11.2 Schematic representation of the dispersion of developmental stage of *E. affinis* in the middle part of the Seine estuary (Normandy Bridge) as a function of the mean tidal cycle, based on the results of this study. Width of arrows at the top of the figure represents the magnitude of the water velocity during a length of time represented by their length. The different water masses have been identified at the bottom of the figure as a function of the salinity range according to McLusky (1989): oligohaline zone [0.5–5], mesohaline [5–18] and polyhaline [18–25]. The population abundance increase during the ebb with low constant resuspension and hypothetical migration of adults (oval) and copepodids (square) that dominate the population from the poly- to mesohaline zone in surface and bottom water. In the oligohaline zone around the low slack, when current velocity is low, nauplii dominate the population. At the beginning of the flood when current velocity is maximal, the population is resuspended and adults and copepodids start to migrate (according to the hypothesis of Morgan et al., 1997 and Schmitt et al., unpublished data) to the bottom water while the current is decreasing. *Source:* Figure 9 from Devreker et al. (2008).

Seine estuary while maintaining position within its preferred salinity range.

Temperature is another variable that influences estuarine zooplankton on short-term and long-term time scales. The annual succession in copepod species composition may be driven by temperature (Mauchline, 1980) as well as salinity. Egg production and growth rates are also strongly temperature dependent (Gillooly, 2000). In temperate estuaries, reproduction by benthic bivalves such as oysters, resulting in the release of meroplanktonic larvae, is often triggered by rising water temperatures (Ingle, 1951).

11.5 ESTUARINE DISTRIBUTIONAL PATTERNS

It is extremely difficult to assemble an accurate estimate of the distributional patterns of any estuarine zooplankton species. Through the influence of the tides, organisms are continually shifting landward or seaward. Moreover, it takes time to collect samples. Depending upon the size of the estuary and the sampling resolution, it may take several days to assemble a composite picture of the distributions of organisms throughout the entire system. Toward the extremes of an organisms' distribution, animal densities may be too low for their abundances to be reliably estimated unless the volume filtered by the plankton net is large enough. All of these factors mean that the resultant maps are, at best, an approximation of the true synoptic distributional patterns of the constituent taxa.

In spite of the importance of estuarine zooplankton, and perhaps given the challenges that we have just summarized, there are relatively few publications that report the distributional patterns of mesozooplankton with high spatial and taxonomic resolution in relation to hydrographic parameters. Zhang et al. (2006) used an undulating vehicle equipped with

a conductivity-salinity-depth (CTD) and an optical plankton counter (OPC) to map the distribution of zooplankton biovolume along the axis of the Chesapeake Bay during three seasons from 1996–2000. The OPC is an instrument that measures the interruption of a light beam by particles to estimate the abundance and sizes of zooplankton and other particles; however, it cannot determine the identities of each particle. Zhang et al. (2006) demonstrate the dynamic and patchy nature of estuarine zooplankton distributions albeit in a taxonomically ambiguous manner. Their study also demonstrates how time consuming sampling a large system can be, even when using a towed, semiautomated sensing system such as the OPC.

Available data indicate that the horizontal distribution patterns of zooplankton are by no means static. Individual species are concentrated within waters that contain conditions favorable for growth and reproduction. As mentioned earlier, salinity is an important determinant of the spatial distributions of most zooplankton. An example of how salinity influences the distribution of zooplankton comes from research by Peitsch et al. (2000) in the Elbe River Estuary, Germany. This example is also based on the copepod *E. affinis*. In the Elbe River estuary, *E. affinis* is the numerically dominant mesozooplankton species accounting for 90–99% of the numerical abundance throughout the year. It is an oligohaline species with peak abundances in waters <0.5 psu (Peitsch et al., 2000). The strength of the river discharge shifts the oligohaline region of the estuary seaward during years of high flow, and landward when flows are low. The displacement of favorable habitat for *E. affinis* can be observed in a plot of abundance relative to salinity along the estuary (Fig. 11.3). During periods of low river discharge (09/87, 04/93, and 07/94) there was a shallow salinity gradient and *E. affinis* was distributed upstream. Conversely, when river discharge was high, the population was shifted seaward. Steep salinity gradients produced a sharp cutoff in the abundance of *E. affinis*, while in shallower gradients the decline in abundance was more gradual and the species had a broader distribution. This example illustrates how many estuarine species may shift their distributions seaward or landward as waters of favorable salinity ranges are shifted by precipitation or other forcing factors.

During extreme precipitation and runoff events (e.g., tropical storms, floods), rapid seaward currents can flush planktonic organisms out of estuaries. Some evidence of how copepods are adapted to repopulate estuaries was provided by Ueda et al. (2004) during routine zooplankton sampling in the tidal region of the Chikugo River, Japan. This sampling fortuitously encompassed a period of heavy rain coupled with the opening of an upstream reservoir. These events created a strong, net seaward flow that flushed the majority of the population of the dominant copepods *Pseudodiaptomus inopinus* and *Sinocalanus sinensis* out of the system. Sediment sampling in the channels off the mouth of the Chikugo River revealed that many *P. inopinus* copepods were aggregated in a thin layer immediately above the bottom. Moreover, these copepods were almost entirely adults, which would be capable of stronger swimming responses. No *S. sinensis* were detected in these samples. *Sinocalanus sinensis* were likely displaced further seaward and they were subsequently detected in bottom samples during flood tides. By aggregating in a thin layer adjacent to the sediments, *P. inopinus* were hypothesized to be exploiting a low current velocity refuge that was well placed for a return to the estuary on the following flood tide where they would rebuild their population through reproduction. In cases where zooplankton are unable to return to the estuary from which they were flushed, they may be replaced by more rapidly growing species. In such cases, copepods would tend to be replaced by rotifers.

11.6 SEASONAL ABUNDANCE AND PRODUCTION PATTERNS

One of the most important factors affecting the rate of population growth for a species is its generation time (Cole, 1954). This is the time required for an organism to develop from an egg to a mature adult. Most estuarine microzooplankton and mesozooplankton have very short generation times and are able to rapidly increase their numbers when conditions are favorable. For example, in the laboratory the marine copepod *Acartia clausi* completed its development in 14 days under laboratory conditions (Iwasaki et al., 1977) and many copepods have generation times of 20–30 days (Ianora, 1998). The generation times of microzooplankton are even more rapid than mesozooplankton. Although the generation time varies by species and is influenced by a variety of factors, Gillooly (2000) provides some general relationships that predict generation time as a function of body size and temperature for a variety of zooplankton taxa (rotifers, copepods, and cladocerans).

Fluctuations in the abundances of estuarine zooplankton in general, and copepods in particular, appear to be linked to fresh water discharge. In regions where there is a pronounced wet and dry season, zooplankton may increase in abundance in
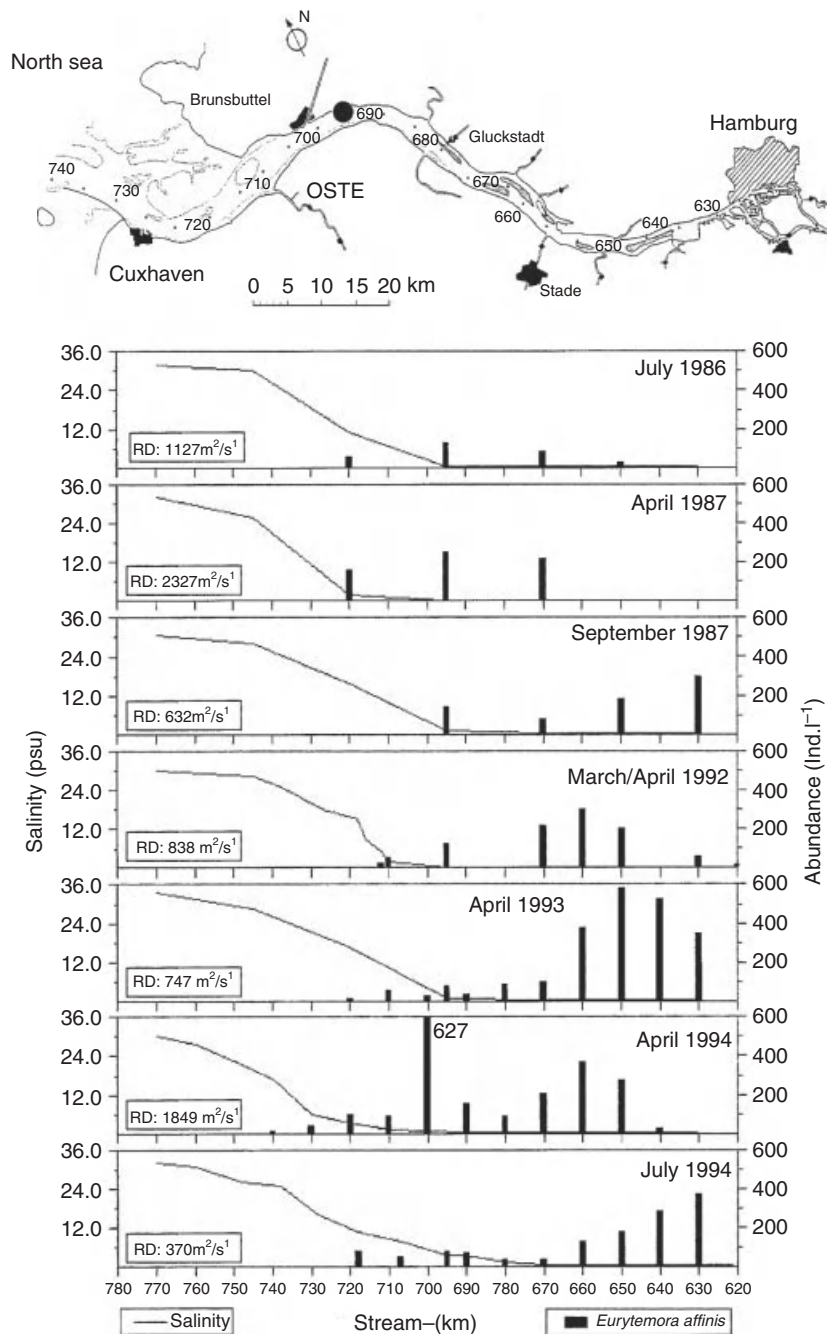
FIGURE 11.3 Salinity and abundance *of E. affinis* in the Elbe Estuary during longitudinal sampling (RD = mean river discharge of the 20 days before sampling). The map of the Elbe Estuary shows the distance downstream from the source (numbers = stream kilometers) and the black dot indicates the anchor station, located at stream-km 695. *Source:* Figure from Figures 1 and 9 of Peitsch et al. (2000).

response to precipitation and runoff. The putative causal relationship is an increase in nutrient concentrations that stimulate phytoplankton blooms, which trigger increased production by microzooplankton and mesozooplankton. Given the preference by copepods for microzooplankton prey over phytoplankton

(Gifford and Dagg, 1988; Rollwagen-Bollens and Penry, 2003), elevated grazing by copepods on microzooplankton may reduce grazing rates on phytoplankton and thereby enhance the standing stock of phytoplankton. Such a mechanism could account for observations of enhanced copepod abundances

during the wet season in many estuaries. Pulsed discharges of water into estuaries may also enhance zooplankton production by improving the variety and nutritional value of their prey. Episodic fresh water inflows may prevent competitive exclusion among phytoplankton and lead to a more diverse phytoplankton assemblage (see summary by Miller et al., 2008). This may provide zooplankton with a more diverse and nutritious array of phytoplankton prey with consequent higher productivity.

11.7 LATITUDINAL GRADIENTS

The physical properties of estuarine systems exhibit substantial variability over latitudinal gradients from high to low latitudes. Seasonal temperature cycles, temperature ranges, day length, and precipitation patterns are a few of the factors that are influenced by latitude. Given the sensitivity of zooplankton to changes in hydrographic factors, it would be reasonable to assume that changes in latitude would indirectly influence zooplankton community composition. Moreover, submergent and emergent aquatic vegetation types vary with latitude. Changes in these important nursery habitats influence the relative abundances and species composition of zooplanktivorous fishes, and therefore may indirectly influence the diversity and seasonal abundance cycles of zooplankton. Unfortunately, there are relatively few studies that address how zooplankton vary over large latitudinal gradients, perhaps due to the challenges of conducting comparative research over a sufficiently broad geographical sample of estuaries. Still, there are several studies that can illustrate how some zooplankton taxa vary along latitudinal gradients.

Dolan and Gallegos (2001) provide evidence that species richness of estuarine tintinnids (small microzooplanktonic ciliates) is maximal near the equator and declines linearly toward both poles. While they did not provide any mechanistic explanation for the pattern, the relationship was linear suggesting that it was driven by some factor that varies in a linear manner with latitude. Tintinnids are important prey for copepods, the latter of which were the subject of a review by Turner (1981). He examined species diversity of calanoid and cyclopoid copepods over a broad latitudinal gradient in the northern hemisphere from the Arctic to subtropics. There was no clear relationship between species richness of calanoid copepods over the range of latitudes examined; however, species richness peaked in temperate latitudes

(30–50 °N). Cyclopoid copepods displayed a different pattern with species richness being very low in higher latitudes and increasing to a maximum in subtropical latitudes (south of 35°N). Turner (1981) identified several groups of species with distinct latitudinal distributional patterns. The peak in calanoid species richness within temperate regions was attributed to the presence of these species groups in the estuaries at different times of the year.

11.8 TROPHIC INTERACTIONS

Estuarine food webs can be represented by generalized marine food webs that include primary producers, primary consumers, and a series of trophic linkages culminating in top predators (Fig. 11.4). Included in such food webs is a recycling step involving dissolved organic carbon (DOC), heterotrophic bacteria, and microzooplankton, termed the *microbial loop*. Zooplankton generally occupy the lower strata of estuarine food webs, although some cnidarians and ctenophores may be important predators in some systems. Sources of food for estuarine zooplankton include phytoplankton, detrital material from terrestrial plants, emergent macrophytes, submerged aquatic vegetation, and pollen. In addition, phytoplankton from marine sources may also be abundant in the lower regions of estuaries while fresh water phytoplankton provide an energy subsidy to the upper regions of an estuary. In addition, DOC from all of these plant sources may be utilized by heterotrophic bacteria. In many estuarine systems, turbidities are high, which can reduce light penetration. Whether or not the reduction in light reduces primary production by phytoplankton depends upon the depth of the estuary and the degree of mixing. Where production is reduced by turbidity, the highly nutritive phytoplankton food may not be as prevalent as detrital material from other plant pools.

Certain regions of estuaries are particularly important foraging regions for zooplankton. One of these is the ETM zone. The ETM is a region of strong interaction between fresh and salt water, which generally occurs at the landward limit of salt water intrusion. Turbulence generated by tidal currents flowing over the bottom leads to resuspension of benthic sediments, while mixing of the overlying fresh water with the underlying salt water causes suspended particles to flocculate and sink. These two processes combine to produce a zone that is characterized by elevated turbidity, high particulate loadings, and strong horizontal gradients in

salinity. Circulation patterns produce a convergence near the bottom that leads to an accumulation of particulates and of zooplankton. In addition to the high concentration of particulates that are rich in bacteria, the ETM can also contain abundant phytoplankton derived from *in situ* production and allochthanous upstream fresh water sources. Thus, the ETM provides an enhanced foraging ground for zooplankton.

Within the ETM, copepods can attain very high abundances. For example, Winkler et al. (2003) estimated the abundance of the copepod *E. affinis* at 25,000 m^{-3} in the St. Lawrence River estuary ETM during late June. On the basis of measurements of body mass and carbon content and carbon-specific ingestion rates, they estimated that this population of copepods consumes approximately 50 T of phytoplankton carbon per day during late June and early July. Other studies support the importance of copepods as grazers within the ETM but demonstrate the importance of other taxa such as mysids as grazers (Fig. 11.4). Roman et al. (2001) reported abundances of *E. affinis* from the bottom waters of the Chesapeake Bay ETM of over 200,000 m^{-3}. These abundances were from acoustically derived measurements and Niskin bottle samples.

Global climate change has the potential to alter trophic interactions in estuarine systems by altering the timing of seasonal abundance patterns. Planktonic communities may be particularly sensitive to small mean annual increases ($\sim$1 °C) in water temperature (Oviatt, 2004) because individual species respond differently to altered climatic patterns. One

example of this may be seen in Narragansett Bay, USA, where the lobate ctenophore (*M. leidyi*) and calanoid copepod (*Acartia tonsa*) are dominant members of the planktonic community (Costello et al., 2006). *M. leidyi* feeds on *A. tonsa* and other prey items and has the potential to drastically reduce the abundance of *A. tonsa* via predation. Both *A. tonsa* and *M. leidyi* dominate in summer with the former peaking during spring–summer and the latter during late summer and early fall. Both species decline to low abundances during winter with *M. leidyi* overwintering in shallow bay areas while *A. tonsa* eggs overwinter in deeper regions of the bay. As mean annual water temperatures have been warming in Narragansett Bay, the date of first appearance of *M. leidyi* at central bay stations has advanced by 59 days over the period 1951–2003 (Costello et al., 2006). Over the same period, the phenology of *A. tonsa* has not changed significantly. The differential response is presumably because the shallower waters where *M. leidyi* overwinters are more sensitive to warming and ctenophore egg production is temperature dependent. As a consequence, the peak abundance of the predator *M. leidyi* has become more closely matched to that of *A. tonsa* and extends into a period when the copepod previously enjoyed a refuge from ctenophore predation (Fig. 11.5). In response to this shift, the peak abundances of *A. tonsa* have significantly declined since 2000 (Fig. 11.5; Costello et al., 2006). This change has implications for the entire planktonic food web in Narragansett Bay where other organisms are dependent upon *A. tonsa*.
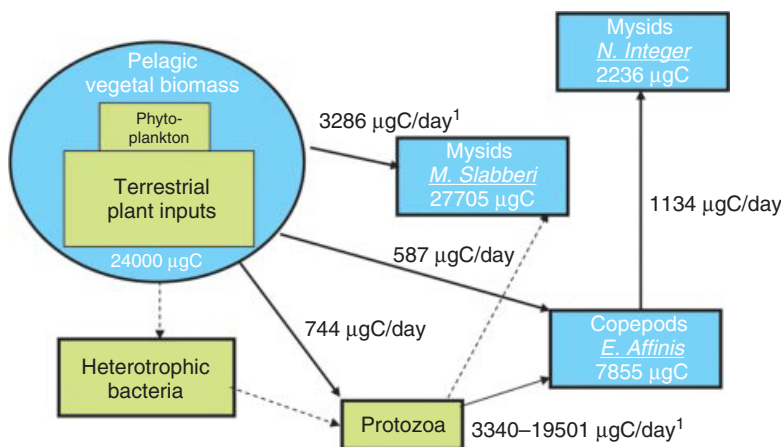
FIGURE 11.4 An example of an estuarine planktonic food web from within the turbidity maximum zone of the Gironde River estuary in July 2002 showing biomass and flux expressed as μgC/m^3 and μgC/m^3/ day, respectively. Estimation of such a food web requires careful measurement of the standing stocks within each pool and grazing rate experiments to quantify the magnitudes of fluxes among consumers. *Source:* From David et al. (2006).
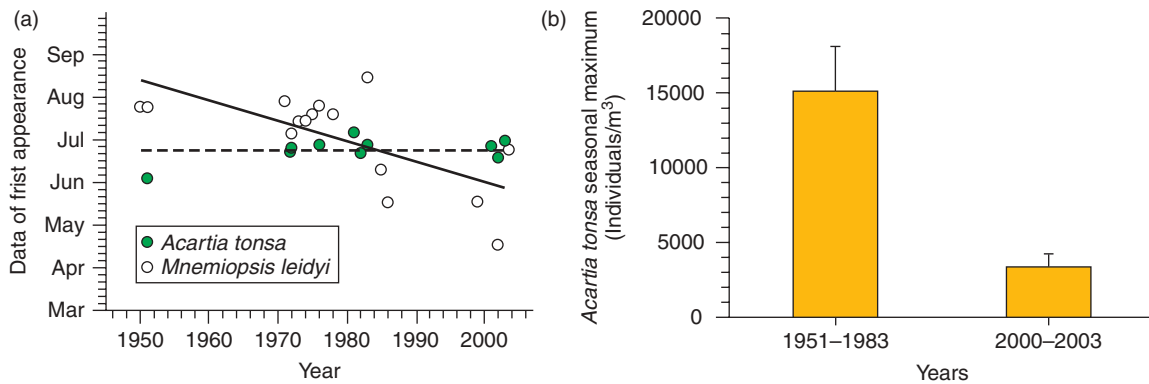
FIGURE 11.5 (a) Historical patterns in phenology of *A. tonsa* and *M. leidyi* at central estuary stations in Narragansett Bay, USA. Linear regression indicates that *A. tonsa* phenology has not shown significant alteration ($p = 0.195$) during the period from 1950 to 2003. In contrast, the first appearance of *M. leidyi* has shifted significantly ($p = 0.006$) earlier in the year during the same period. (b) Decline in maximum seasonal concentrations of the copepod *A. tonsa* in the Narragansett Bay estuary during the period 2000–2003 ($n = 4$) relative to years between 1951 and 1983 ($n = 7$). All data collected from the same site; historical data (pre-2000) assembled from a variety of sources. Error bars represent standard error of the mean and, although not shown, negative bars are symmetrical with positive bars. Average values for the two time periods are significantly different (Mann Whitney, $p = 0.008$). *Source:* From Costello et al. (2006).

11.9 PREDATION

The size of zooplankton, in part, determines what organisms they are vulnerable to. Larger taxa are usually both more conspicuous and possess greater escape capabilities. Zooplanktivorous fish are important predators of copepods, mysids, and other large estuarine zooplankton. Predation by zooplanktivorous fish is usually more intense in regions where turbidity is reduced, allowing more effective visual foraging. Mesocosm studies in a coastal fjord in Denmark demonstrated that zooplanktivorous fish were responsible for significant reductions in the abundances of holoplanktonic zooplankton such as the copepod *A. tonsa* and the cladoceran *Pleopis polyphemoides* (Horsted et al., 1988). Microzooplankton including tintinnids were preyed upon by suspension-feeding bivalves *Mytilus edulis* but were not impacted by fish owing to their small size. The larger holoplankton were unaffected by bivalves because they presumably were able to detect and avoid the incurrent siphon flowfields.

Ctenophores, particularly *M. leidyi*, are voracious consumers of copepods and other zooplankton. Condon and Steinberg (2008) found that calanoid copepod densities were inversely related to *M. leidyi* biomass in the York River estuary—a subsystem of Chesapeake Bay. These nonvisual predators can consume copepods and other prey in turbid waters that would otherwise offer some refuge from visual predators such as fishes. In the Chesapeake Bay, densities of *M. leidyi* are also under the control of gelatinous predators such as the medusa *Chrysaora quinquecirrha* (Condon and Steinberg, 2008) and potentially other medusa species as well as the lobate ctenophore *B. ovata*. The absence of natural predators in systems where *M. leidyi* has been introduced likely explains why this species has undergone such dramatic population explosions.

11.10 RECRUITMENT

Many of the meroplanktonic organisms in estuaries are the larvae of species that spawn outside of estuaries. Since most estuaries have a riverine and oceanic terminus, these larvae may originate from fresh water species that spawn in the upper reaches of estuaries, such as the fresh water shrimp genus *Macrobrachium*, or marine species that spawn near or outside the mouth of estuaries, such as the blue crab *Callinectes sapidus*. Marine-sourced larvae predominate in most systems.

Estuarine-dependent larvae living in shelf waters face two challenges in getting back to an estuary. The first is crossing the shelf and moving toward the coast so that they are located near an estuarine mouth. The second challenge is to successfully gain entrance to an estuary. Much research has been devoted to these two topics and a consensus is beginning to develop on the factors that are responsible for successfully achieving cross-shelf transport and estuarine ingress. Successful larval recruitment appears to require a combination of favorable physical and behavioral processes.

Cross-shelf transport is often facilitated by onshore circulation driven by favorable winds. On coasts where upwelling predominates, relaxation of upwelling-favorable winds can cause onshore movement of the surface layer, which brings larvae toward the coast (Roughgarden et al., 1991). Onshore Ekman transport induced by favorable winds can raise the slope of the waters close to the coast, producing flows toward the coast and estuaries (Epifanio, 1995). Internal tidal bores propagating onshore can transport larvae toward the coast (Pineda, 1994). Larvae capable of stronger swimming likely undertake directed movement as has been reported for larvae of American lobsters *Homarus americanus* (Cobb et al., 1989) and palinurid lobsters (Jeffs et al., 2005).

Gaining access to an estuary is also likely to be due to a combination of adaptive larval behaviors combined with physical transport processes and events. Selective tidal stream transport (STST) describes the interaction of larval behaviors, and physical processes which place larvae in the water column during flood tides and near or on the bottom during ebbs. This tide-hopping behavior has the net effect of progressively advecting larvae into estuarine systems. Much recruitment occurs on nocturnal flood tides, and a series of cues that can produce such an effect have been experimentally evaluated. As a flood tide commences, a stationary larva located on the bottom would experience an increase in hydrostatic pressure, salinity, and turbulence (Queiroga et al., 2006). These cues are assumed to trigger an ascent into the flood tide water column, although, curiously, it is not yet known how invertebrate larvae lacking a compressible structure actually sense a change in hydrostatic pressure. Once in the water column, larvae need a cue that tells them when to drop out of the water column to avoid being advected seaward. A larvae moving in a parcel of water would have little ability to detect changes in salinity or pressure, so a reduction in turbulence associated with the onset of slack water has been proposed as a cue to drop out of the water column. Swimming during the ebb tide is inhibited by chemical cues associated with organic compounds of estuarine origin. Finally, inhibition of swimming during daytime flood tides by higher light intensities would reduce the number of larvae present in daytime flood tides. Much of the work on these issues has been conducted on crab larvae (Forward and Rittchoff, 1994, Forward et al., 1997; Tankersley et al., 1995; Forward and Tankersley, 2001).

11.11 SAMPLING ZOOPLANKTON

Zooplankton distributions are highly patchy. As a consequence, variation among replicate net tows is likely to be very high. Gagnon and Lacroix (1981) collected 347 vertical net samples over a period of 175 h from a fixed station in the upper St. Lawrence River estuary. They estimated the 95% confidence interval for a single observation to be 37–268% of the mean copepod abundance. For some taxa such as *Calanus finmarchicus* and *Eurytemora herdmani* this variability was even higher: 11–900% and 20–487%, respectively. This high variability was attributed to longitudinal tidal displacements combined with periodic vertical fluctuations in the depth of the pycnocline induced by internal tides. What their data mean to anyone attempting to quantify the distribution and abundance patterns of zooplankton in an estuary is that they have a challenging task ahead of them.

Devices for sampling zooplankton include bottles, nets, pumps, and traps. More recently, we have seen the emergence of optical systems including particle counters and imaging cameras as well as single and multifrequency echosounders. See Wiebe and Benfield (2003) for a detailed examination of the various systems available to sample zooplankton.

Although microzooplankton may be collected using fine-mesh nets, slow pumps, or water bottle samplers, comparisons of these gears (James, 1991) indicate that large-volume water bottles ($\sim$3 l) from which subsamples (150–250 ml) were settled over 48 h provided the greatest recovery efficiency of small ciliates. This technique was superior to screening the contents of water bottle samples through a 20-μm mesh compared to collection using a slow velocity pump (6 l/min) that passed water through a 20-μm mesh, or vertical net tows using a 20-μm mesh net. Screening water samples from bottles through a 20-μm mesh screen should be avoided as it resulted in the loss of 99% of ciliates <50 μm (James, 1991). Preservation of samples with Lugols iodine and mercuric chloride provided significantly higher recovery of ciliates <50 μm than formalin or gluteraldehyde (James, 1991).

One of the new instruments that shows a great deal of potential as a means of quantifying microzooplankton in fresh or preserved samples is the FlowCAM (Sieracki et al., 1998). This laboratory instrument is a flow-through, imaging microscope that detects, images, and measures particles in the size range encompassing phytoplankton, microzooplankton, and small mesozooplankton. Examples of images from the FlowCAM are illustrated in Figure 11.6.

FIGURE 11.6 Examples of phytoplankton and microzooplankton from Louisiana estuaries imaged with a color FlowCAM. Most particles were imaged at 10 or 20× magnification.

Preserved mesozooplankton collected with nets or pumps can be enumerated using a Zooscan system (Grosjean et al., 2004). The Zooscan is a waterproofed scanning system that permits samples to be digitized and measured at high resolution (Fig. 11.7). The contents of scans are isolated into individual images called *vignettes*, which can be subsequently sorted visually and classified or classified semiautomatically using computer-based classification algorithms (Benfield et al., 2007).

Nets remain a core means of enumerating mesozooplankton. They range from simple nonopening/closing systems to multiple net systems equipped with environmental sensors controlled from a shipboard computer. Simple plankton nets have the advantage of being relatively inexpensive and easy to use. Flow meters permit the estimation of the volume filtered. Nets suffer from several disadvantages. They are prone to clogging and care must be taken to ensure an adequate surface area:frontal area ratio. Nets integrate the abundance of organisms along their tow path and cannot provide

data on the distributions of organisms along their trajectory. Nets may damage fragile taxa, particularly gelatinous organisms. Most nets are not designed for high speed sampling, and larger, more mobile zooplankton may detect and avoid the net. They do have the advantage of providing a physical sample of zooplankton, which may be essential for studies requiring high taxonomic resolution, physiological data about lipid or RNA/DNA ratios, or genetic information. Multinet systems such as MOCNESS (Wiebe et al., 1985), BIONESS (Sameoto et al., 1980), or the Multinet provide a means of collecting vertically or horizontally stratified samples; however, their size and vessel deployment requirements may preclude their use in many smaller estuaries.

Pumps have the advantage of resolving vertical distributions on finer scales than nets. When equipped with flowmeters, pumps are capable of more precise measurement of the volume sampled and their design permits the use of different mesh sizes (Dixon and Roberson, 1986). See Miller (1985) and Powlik et al. (1991) for reviews of pump designs. Both Coughlan
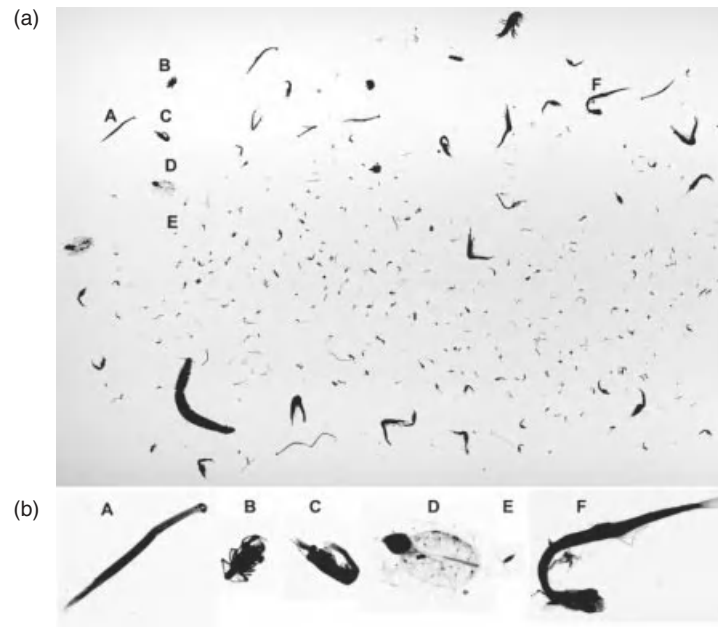
FIGURE 11.7 (a) An estuarine plankton sample from Louisiana digitized with a Zooscan. (b) Magnified vignettes of different organisms (A, chaetognath; B, crab megalopa; C, decapods; D, doliolid; E, calanoid copepod; F, fish larva).

and Fleming (1978) and Dixon and Robertson (1986) provide examples of small pump samplers designed for use in estuarine systems.

Optical systems can be divided into particle-counting systems and imaging systems (Wiebe and Benfield, 2003). Optical systems suffer from inherent limitations in turbid waters; however, particle counters such as the OPC and its derivative—the laser optical plankton counter (LOPC) have been used in estuaries to document the spatial distribution of mesozooplankton on much finer horizontal and vertical scales than those possible with nets. These systems have relatively short optical path lengths, which permit their use in moderately turbid waters, although interference from detritus may be a problem (Zhang et al., 2000). Both the OPC and LOPC measure the size of particles that pass through a light sheet. The OPC produces size–frequency estimates of equivalent spherical diameter but cannot produce taxonomically explicit information about the nature of the particles it detects and the user must interpret the size frequency distributions to infer the composition of the measured zooplankton assemblage. The LOPC has a faster analog to digital converter that provides an estimate of the shape of the particle passing through the laser sheet. In this way, the user is provided with more information about the potential identity of each particle. OPCs and LOPCs have been used in relatively clear fjord systems (e.g., Wieland et al., 1997; Halliday et al., 2001); however, they have

also been used to study zooplankton in more turbid systems such as the Chesapeake Bay (Roman et al., 2005; Zhang et al., 2006). Imaging systems employing cameras are generally ineffective in turbid estuarine systems because scattering by suspended sediment and phytoplankton degrades image resolution. There have been successful attempts to constrain the image volume to a small path length by placing a 35-mm camera and strobe within the cod end of a net (Olney and Houde, 1993).

11.12 HUMAN IMPACTS

11.12.1 Introduced Species

The introduction of zooplankton from one system into another can have a profound and adverse impact on the ecology of the affected system. In the absence of natural predators and other controlling factors, introduced species may proliferate and dramatically alter existing community structure with impacts that extend to multiple trophic levels. Introductions may be accidental or intentional; however, the transfer of very large volumes of water in the ballast of commercial ships has proved to be an effective accidental means of introducing exotic species into estuarine systems around the world. In the San Francisco estuary, Cohen and Carlton (1998) estimated that aquatic species were being introduced via ballast

water transfers at the rate of one new species every 14 weeks after 1969. While not all of these introductions represent zooplankton, many were transported as meroplanktonic larvae in ballast water.

The introduction of the ctenophore *M. leidyi* from North American estuaries into the Black Sea and Azov Sea during the 1980s is an example of how an exotic species can rapidly alter the systems into which they have been introduced (Kideys, 2002; Oguz et al., 2008). Moreover, the establishment of *M. leidyi* in the Black Sea illustrates how other anthropogenic impacts such as eutrophication and overfishing can exacerbate the impact of an introduced species on an ecosystem. *M. leidyi* was first detected in the Black Sea in 1982 and subsequently underwent a rapid population increase. By the end of the decade, *M. leidyi* had replaced the anchovy *Engraulis encrasicolus* as the top predator in the Black Sea (Oguz et al., 2008). During the 1990s, *M. leidyi* populations underwent several declines and increases. Environmental factors such as a particularly cold period combined with introduction of another ctenophore (*B. ovata*), which is a natural predator of *M. leidyi*, were associated with declines in the abundance of the latter and the gradual recovery of anchovy stocks.

Gelatinous zooplankton are not the only examples of introduced zooplankton. Ballast water often contains abundant and diverse zooplankton assemblages (Cordell et al., 2009). In a study of the zooplankton in ballast water from ships docking in Puget Sound, Cordell et al. (2009) identified 124 different taxa. Bivalve larvae were present in almost 50% of all samples, while species of the calanoid copepod *Acartia* and cyclopoid copepod *Oithona davisae* were present in about 32% of samples and barnacle cyprid and nauplii were present in 26 and 21% of samples, respectively. Even at low densities of a few individuals of a species per cubic meter, the large volume of water discharged by ships (mean of 9.5 million m^3 per year in Washington State), implies that there is a high potential for the introduction of new species. Because it is so difficult to remove introduced species, the focus is on preventing their release in the first place.

How introduced species interact with endemic zooplankton ranges from competition for resources to direct predation. Kimmerer et al. (1994) provide evidence that a clam (*Potamocorbula amurensis*), which was introduced to San Francisco Bay in 1986 from eastern Siberia, was responsible for declines in the abundance of the copepod *E. affinis*. The mechanism behind the decline appeared to be direct predation by the filter-feeding bivalve on the copepod nauplii.

11.12.2 Eutrophication and Pollution

The addition of nitrogen and phosphorus to estuarine systems typically produces an increase in primary production by diatoms and other phytoplankton. In addition to stimulating a bloom of phytoplankton, this increased production results in the release of additional dissolved organic matter in the form of algal exudates. This DOC stimulates bacterial production, which leads to a bloom of microplanktonic (primarily protist) grazers. At this point, there are at least two potential outcomes depending upon the fate of the excess phytoplankton production. If the increase in phytoplankton food availability falls within the food-limitation range of copepods and other crustacean grazers, then the stocks of these grazers should increase and graze down the excess phytoplankton production (Capriulo et al., 2002). On the other hand, if grazers cannot consume much of the excess production, then bacterial decomposition of dead phytoplankton biomass will stimulate additional microplanktonic production and the combined effect of the bacterial and microzooplankton respiration will reduce water column dissolved oxygen, which will suppress mesozooplankton biomass and production. The latter outcome seems to be more common (e.g., Zervoudaki et al., 2009) than the former, perhaps in part due to the differences in the generation times of phytoplankton, microzooplankton, and mesozooplankton.

Eutrophication is frequently associated with low dissolved oxygen conditions that can directly impact the abundance and species composition of estuarine zooplankton. In the Bilbao estuary, Spain, improvements in wastewater treatment and a decline in industrialization resulted in higher dissolved oxygen concentrations over the period 1999–2001 compared to the early 1980s (Albaina et al., 2009). The improved water quality was accompanied by the occurrence of new species of copepods (*Calanipeda aqua-dulcis* and *E. affinis*) and the establishment of several species of *Acartia*. At the same time, the composition of the zooplankton community in the Bilbao estuary began to more closely resemble that of the nearby and relatively pristine Urdaibai estuary (Albaina et al., 2009).

There is some evidence that changes in water column dissolved oxygen can directly impact the distribution patterns of certain zooplankton taxa. For example, the copepod *E. affinis* is a euryhaline species that occurs over a wide range of salinities (Lee, 1999); however, its ability to tolerate low salinities is reduced at low oxygen concentrations. In the Schelde estuary, Netherlands, Appeltans et al. (2003) documented a shift in the distribution of *E. affinis* from a brackish to

fresh water region over several years that appeared to coincide with an increase in water column dissolved oxygen concentrations in the fresh water region.

Zooplankton may be particularly sensitive to inorganic and organic pollutants. In fact, the standard USEPA toxicity bioassay utilizes mysids (*Mysidopsis bahia*) as test organisms (USEPA, 1996). While such laboratory tests are useful for estimating lethal effects of toxicants, they provide little insight into how pollutants in estuaries impact the resident zooplankton. The impact of any pollutant depends on the dose, which is dependent upon exposure time and concentration, both factors that can vary substantially in the dynamic environment of an estuary. Studies of mixed zooplankton assemblages in mesocosms of different volumes ($1.5-30$ m^3) treated with additions of mercury produced increased mortality of copepods (Kuiper et al., 1983). This suggests that acute exposure to high concentrations of pollutants will lead to high mortalities. A review of data from oil spills support the existence of high mortality that is generally followed by rapid recovery due to the short generation times of zooplankton (Kennish, 1997).

The impacts of pollutants may also be subtle. At sublethal concentrations, anthropogenic compounds may still influence the distribution of planktonic organisms. A laboratory study using a choice chamber demonstrated that postlarval brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) were capable of detecting and avoiding the compound pentachlorophenol at concentrations that were well below levels that would induce mortality (Benfield and Aldrich, 1994). Moreover, the presence of sublethal trace amounts of pentachlorophenol were capable of suppressing previously demonstrated attraction to estuarine water (Benfield and Aldrich, 1992). Such findings suggest that the presence of sublethal concentrations of some pollutants may effectively alter distributional patterns of zooplankton in estuaries if they find such waters repellent and actively avoid them, or alter their behaviors in such waters in a nonadaptive manner.

11.12.3 Fresh Water Diversions and Dams

Construction of dams for hydroelectric, water conservation, or salt water control purposes can dramatically alter the normal hydrological cycle, salinity distribution, and current velocities within an estuary. How zooplankton respond to these alterations is highly site dependent. In the Senegal River estuary, the construction of the Diama dam in 1985 appears to have altered the abundance, composition, and distribution patterns of zooplankton in the system (Champalbert et al., 2007). In comparing their results with a preconstruction study, which employed the same sampling gear, Champalbert et al. (2007) noted an increase in overall mesozooplankton abundance after construction of the dam by 1 order of magnitude. This increase was attributed to increased eutrophication in what had been an oligotrophic estuary. After construction of the dam, zooplankton abundances increased toward the dam, whereas prior to its presence, abundances had increased toward the estuary mouth.

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ESTUARINE BENTHOS

James G. Wilson and John W. Fleeger

12.1 INTRODUCTION

The association of humans with estuaries goes back millennia, as indicated by the location of ancient settlements and the remains of their diet, which included organisms such as oysters and mussels. Mussels and oysters are members of the estuarine benthos, a numerically abundant if somewhat low diversity group that makes up by far the major part of consumer biomass in estuaries. Benthic organisms are important in the food web of estuaries and some are important fishery species. In this chapter, we describe the characteristics of this group, look at the factors that control their abundance and distribution, and discuss their importance in the estuarine ecosystem.

Benthos is a collective term for organisms living in or on the bottom (Fig. 12.1) and includes both producers (phytobenthos) and consumers (zoobenthos). Benthic animals (the focus of this chapter) can be further defined based on life habit or size (e.g., Friedrich, 1965, Table 12.1). *Epibenthos* and *hyperbenthos* have been used as terms for mobile organisms such as shrimps, mysids, and copepods that move freely between the sediments and the overlying water column (Table 12.1). Benthic organisms are also classified into *infauna* (or endo-), which denotes organisms that dwell in, or more specifically, burrow into, the sediment, and into *epifauna*, which attach to hard substrates such as rock surfaces, mangrove roots, or man-made structures (e.g., pilings). In estuaries, infauna dwell in sediments that vary from fine mud to gravel in subtidal bays and creeks and intertidal systems in vegetated and nonvegetated (i.e., mudflats) habitats. Figure 12.1 shows how a number of characteristic benthic organisms live in and on the sediments.

Benthos is also classified by size, based on practical (sampling) considerations (Table 12.2). However, sometimes animals of the same size may pass through different mesh sizes because of different shapes. Also, juvenile forms of organisms will pass through mesh sizes that adults cannot. Macrobenthos are generally defined as organisms that are retained on a 1- or 0.5-mm sieve (Table 12.2). The use of a 0.5-mm mesh is the current standard, although virtually all older work used a 1-mm mesh. The meiobenthos has representatives of most animal phyla that generally remain in the size range of meiofauna throughout their life (e.g., nematodes), although recently settled larval stages of macrofauna contribute to the meiofauna as do appropriately sized single-celled organisms (e.g., foraminiferans). Microbenthos includes eukaryotic, single-celled forms as well as many prokaryotic consumers.

12.2 SALINITY AND ENVIRONMENTAL VARIATION

Estuaries are highly variable environments. In the estuarine water column and sediments, variation in physical/chemical factors such as temperature,
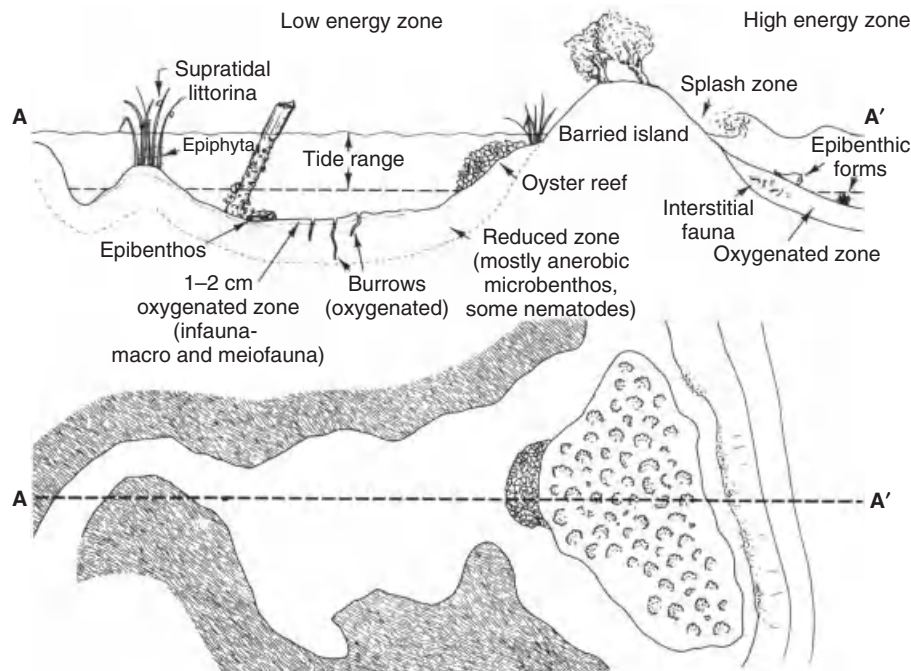
FIGURE 12.1 Diagram representing the various types of estuarine benthos. *Source:* From Day et al. (1989).

TABLE 12.1 Definition of benthos by lifestyle with examples

Term	Definition	Life-habitat	Examples
Epi-(1)	On the surface of	Epipelos—mud Epipsammon—sand Epilithion—rock	Ostracods, triclads, copepods Gastropods, flatfish Barnacles, sea anemones
Epi-(2)	Above the	Moving between sediment and bottom water	Shrimps, mysids
Endo-	Burrowing or living in	Endopelos—mud Endopsammon—sand Endolithion—rock, timber	Bivalves, worms Mobile worms, amphipods, nematodes Shipworm, gribble, paddock
Hyper-	Above the	Moving between sediment and bottom water	Shrimps, mysids
Supra-	Swimming above		Fish—linked through feeding habit

salinity, oxygen, ammonium, and sulfides are high and stressful to biota. The variable salinity regime of estuaries has especially broad implications for benthic communities, and this driver exerts a powerful influence on the biota and the behavior of the system.

Faced with variability of the environment, an organism may either maintain a constant internal state or allow it to follow external changes. These alternative strategies are termed *regulator* and *conformer*, respectively (Fig. 12.2). The balance of these strategies is determined by relative costs and benefits. The cost of regulation is both evolutionary, in the development and maintenance of necessary structures and processes, and bioenergetic, in terms
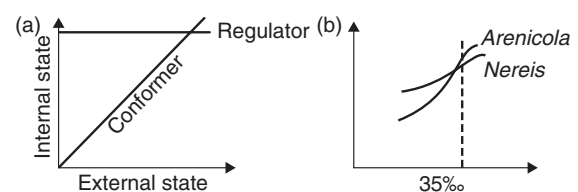
FIGURE 12.2 Regulator and conformer strategies, with typical responses to salinity from benthos: *Nereis* (osmoregulator) and *Arenicola* (osmoconformer). *Source:* From Wilson (1988).

of the energy required to maintain the internal state against external variability. The reward is the optimal

TABLE 12.2 Definition of benthos by size, with references

Term	Definition	Reference
Benthos	All organisms living on or in the sea floor	Baretta-Decker et al. (1998)
Macrobenthos	Retained by mesh of 0.5 mm	Kramer et al. (1994, p. 219)
Meiobenthos	Size between 0.1 and 0.5 or 1.0 mm	Giere (2009)
	Upper limit of size 1- or 0.5-mm mesh	Higgins and Thiel (1988)
	Lower limit commonly 63 μm but sometimes 45-μm mesh	
Microbenthos	Size smaller than 0.1 mm, but see also meiobenthos lower limits	Higgins and Thiel (1988)

operation of physiological functions. Conforming, on the other hand, costs nothing but comes at the expense of metabolic function. In practice, most estuarine organisms display a mix of strategies (Fig. 12.2b), and the degree or range to which regulation or conforming can be a viable strategy may be rather limited. Many estuarine animals are therefore broadly adapted to environmental variation, for example, the Eastern Oyster, *Crassostrea virginica* (Fig. 12.3) can survive and grow from 5 to 42 psu (practical salinity units) and withstand a rapid 15–20 psu change in salinity, but at a fitness cost. The osmoconforming lugworm, *Arenicola marina*, lives from near full-strength seawater (>30 psu) to areas where the salinity rarely exceeds 15 psu in estuaries. However, worms in the lower salinities are smaller in size and weight, and only those in salinities ≥ 20 are able to reproduce, with an exponential decrease in reproduction in salinities below 30.

Remane (1935) hypothesized that because of these challenging physicochemical conditions, macrofaunal marine species diversity declines with salinity (Fig. 12.4) and that true brackish-water species occur at salinities <15 psu. This conceptual model is the foundation for much of our understanding of the distribution of benthos within estuaries. However, salinity variation in some estuaries (e.g., the Baltic Sea) is low, and recent work suggests that variation in salinity may also be an important control over species diversity. Attrill (2002) suggested that increasing salinity variation diminishes diversity, so the rate and scale of salinity change is also important. Because salinity exerts an especially strong control on the pool of biota in estuaries, species available for communities, especially in mid-estuary where salinities are most different from the end members and also salinity variation may be greatest, are the most limited. However, estuaries are also areas of high primary production and input from allochthonous sources, which fuels high levels of biomass and secondary production for those consumers able to deal with the stress.

It is important to note that biological changes related to salinity are not necessarily linear, nor are

FIGURE 12.3 Oyster reef and *C. virginica. Source:* From Day et al. (1989).
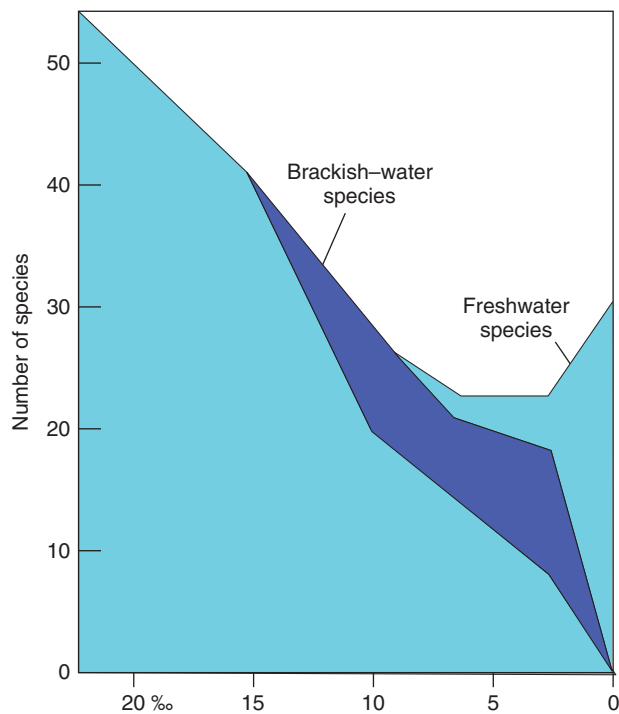
FIGURE 12.4 Remane curves, showing species number and type with salinity. *Source:* From Schlieper (1979).

they correlated along the salinity gradient. Macrobenthic species numbers decline from both end members (river and sea) into an estuary. This decline is neither regular nor symmetrical. The lowest numbers are found in the mesohaline reaches, comprising the true estuarine species. The bulk of the estuarine macrobenthos is of marine origin, in that they classify with other, fully marine species and they are capable of survival in full-strength seawater (e.g., the polychaete *Nereis diversicolor*). There are changes in bottom substrate type along estuaries, and this also plays a part in influencing the distribution of the

biota, as do currents that influence sediment particle size. Gradients of salinity and substratum may alter the relative abundance of infauna within estuaries. For example, macrofauna species diversity and biomass decrease into low salinity reaches of estuaries. Meiofauna, however, experience a decrease in species diversity with decreasing salinity but without a large decline in biomass. Thus, the biomass of meiofauna relative to macrofauna increases in low salinity reaches of estuaries. Some estuaries have little hard substrate (e.g., bar-built estuaries on an alluvial plain), potentially altering the relative proportion of infauna and epifauna. The influence of particle size on the benthos is addressed in the following sections.

Predators and parasites are frequently less tolerant of salinity variation than their prey or hosts. The low and/or variable salinity of estuaries may reduce biological enemies, releasing species able to tolerate low salinity from biological control. The Eastern Oyster (Fig. 12.3) is found at its highest abundance in Louisiana, United States, in salinities below its physiological optimum, as a result of reductions of predation and disease-causing organisms. Thus, areas of estuaries that experience low salinities may act as refuges from harmful biological interactions for many species contributing to high abundances in estuaries.

12.3 BENTHIC FUNCTIONAL GROUPINGS

All major feeding types of benthos can be found in estuaries (Table 12.3). *Deposivores* consume particulate matter and assimilate carbon from in or on the sediment, usually included under the loose heading of detritus, which is particulate organic matter mixed with sedimentary minerals. It includes the remains

TABLE 12.3 Estuarine benthic fauna and functional roles

Group	Size Range (cm)	Individual Life Span	Population Doubling Rate	Functional Roles/Feeding Type	Example
Macro-	0.1–100	1–10 years	1 year	Deposivore Suspensivore Predator Grazer Omnivore	*Arenicola* *Crassostrea* *Callinectes* *Littorina* *Hediste* *Nereis diversicolor*
Meio-	0.0063–0.1	1–6 months	1 month	Deposivore Predator Grazer	*Diplosoma breviceps* *Onyx perfectus* *Desmodora schultze*
Micro-	<0.001	1 month	1 week	Grazer/predator	*Euplotes* spp. *Dactylamoeba* spp.

of other biota and can be derived from both dead plants and animals, but the term also includes other material such as feces, as well as living items such as fungi, microalgae, or bacteria, which can either be unattached, or fixed to the sediment grains themselves, or part of the decomposers engaged in the breakdown of the dead material and feces. Deposivores also ingest benthic microalgae on the sediment surface in shallow areas, particularly if they are nonselective in their feeding habits. *Suspensivores*, also referred to as *filter feeders*, extract their food from the material suspended in the water column, including phytoplankton and zooplankton, as well as any other material in suspension. In areas of high wave energy or turbulence where the rate of resuspension and deposition of sediments is high, the diets of deposivores and suspensivores show a great deal of similarity. Many of the structures or organs for suspension feeding have an outward appearance of a net or filter, but some species may do both (e.g., suspension feed when flow rates are high but deposit feed during slack tides). In almost all animals studied except for crustaceans, the material is taken from suspension with the aid of a mucus covering (to which it may adhere), such that particles as small as individual bacteria (<1 μm in length) can be extracted from the water. Feeding is greatly affected by the size and concentration of particles in the water. Large particles are usually rejected or their entry barred, although recent work has shown that mussels and other suspension-feeding bivalves can take individual zooplankton up to 3 mm in size, although maxima around 450–600 μm are more common.

Functional groupings of estuarine consumers are customarily assigned according to their trophic position (Table 12.3). In practice, however, many estuarine consumers are much more generalized in their feeding habits. For instance, suspensivores often take in a lot of benthic material due to resuspension, and likewise deposit feeders, especially those feeding at the sediment/water interface, take in suspended material, including phytoplankton settling out onto the bottom. *Nereis diversicolor*, an omnivore in Table 12.3, is a classic estuarine opportunist feeder, utilizing whatever food source may be present. It has a pair of strong chitinous jaws, and will actively hunt smaller prey; the mucous lining of its burrow, which is irrigated by the animal's respiratory current, removes material from suspension (and also traps any material brought in from the sediment/water interface), which brings in the possibility of both suspension- and deposit-feeding; and it can also transport dissolved organic matter (DOM, e.g., amino acids) across the body wall. Such differences may lead to great variation in diet from habitat-to-habitat for estuarine consumers (Galván et al., 2008).

For the majority of benthic consumers, feeding type or category is assigned based on structure or morphology—as with *N. diversicolor*, which was long considered a predator. Similar reasoning has been used with nematodes, which have been classified into feeding types depending on their mouth parts (size of buccal cavity, buccal plates, or jaws). These inferred trophic classifications have been challenged by stable isotope evidence, which is better at defining benthic trophic roles. So far, however, evidence suggests that trophic position is much more akin to that of *N. diversicolor*, which consumes a much wider range of food items than initially thought and that dietary contributions vary both in time and in space much more widely than previously assumed. A case in point is the role of marsh grass detritus versus microalgae in the diet of the benthos and hence their respective roles in energy flow in estuaries. An increasing number of studies in the United States suggest that marsh grass (e.g., *Spartina* spp.), despite its abundance, is most important to the diet of only a few animals [marsh periwinkles, the purple marsh crab (*Sesarma reticulatum*), some amphipods, some subsurface infauna, and insects] that live in the marsh proper, while many others (fiddler crabs, and especially species in the creeks) rely more on phytoplankton and benthic microalgae as the basal resource (Sullivan and Moncreiff, 1990; Currin et al., 1995; Carman and Fry, 2002; Fry et al., 2003). Marsh grass is important as a habitat for both prey and predator, although less so in European marshes where the plants are physically smaller and do not extend far down the shore.

The final point to be made about food sources is that most benthic species have the ability to take up DOM against the concentration gradient, and since DOM is plentiful in estuarine water, this may be a good food source. DOM may also be adsorbed by amorphous particles (i.e., mucus produced by microbes or animals) and then consumed.

12.4 BENTHIC ABUNDANCE, BIOMASS, AND SECONDARY PRODUCTIVITY

Both recruitment into and survival of the benthos are strongly affected by stresses of the estuarine environment, and population densities are often very variable. The spatiotemporal variability in density of a number of estuarine benthic species is shown

TABLE 12.4 Feeding type, average life span (years), and CV (SD/mean) of abundances of selected macrofauna time in the Wadden Sea (Beukema et al., 1983)

Species	Feeding Type	Average Life Span (Years)	CV (%)
Scoloplos armiger	Deposivore	1.5	86
Arenicola marina	Deposivore	2	52
Heteromastus filiformis	Deposivore	2	122
Nephthys hombergii	Predator	2	68
Nereis diversicolor	Omnivore	2	93
Lanice conchilega	Suspensivore/deposivore	?3	211
Cerastoderma edule	Suspensivore	5	132
Mytilus edulis	Suspensivore	5	224
Macoma balthica	Deposivore	5	59
Mya arenaria	Deposivore	7	127

in Table 12.4 along with the average life span. The variability of estuarine populations is high, with coefficients of variability (CV) of over 200%. While it might have been expected that the most short lived would be the most variable, the opposite is actually more in evidence. The most short-lived (the polychaete *Scoloplos armiger*) has actually one of the lowest CV (86%), while the highest CV is that of the mussel, *Mytilus edulis*, which may live for more than 10 years (Table 12.4). *M. edulis* is also a suspensivore, as are the other two species with high CV, suggesting that there may be a link between feeding type with community control. Beukema (1988) urged caution in overreliance on numerical metrics of benthos, particularly those based on numbers or biomass, without taking into account the underlying long-term variation at the site.

A contributing factor to the high spatial and temporal variability is the ability of juveniles and adults of many soft-sediment species to disperse. Juvenile bivalves may be suspended and deposited by currents as an aid in finding preferred habitat. For example, the hydrodynamic regime required for transport of the bivalve *Macoma balthica* juveniles is similar to that which produces sediments with the optimum particle size needed to promote fitness for this species (Fig. 12.5, and note the relationship between the current speed and the number and size of individuals being transported). *Hydrobia ulvae* uses surface tension of the water and floats, upside-down, on its extended foot (Fig. 12.6), giving it exceptional powers of dispersal through estuaries. As a consequence of this hydrodynamic transport, the density of *Hydrobia* populations can vary a great deal in both time and space quite independently of the biology of the organism. The distribution and abundance of meiofauna (most of which lack dispersing larvae) are also directly influenced by the hydrodynamic regime. Emergence into the water column by juveniles and
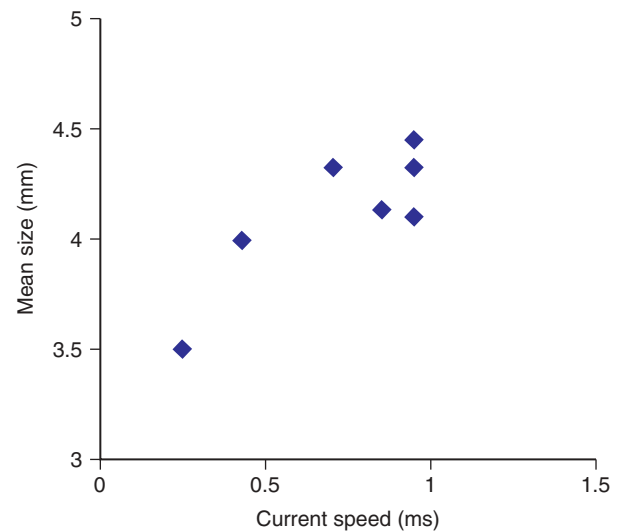
FIGURE 12.5 Mean size (mm) of *Macoma balthica* larvae transported versus tidal current (m/s). *Source:* Data from Beukema and de Vlas (1989).

adults may be passive (by erosion) or active associated with mate finding, feeding, or avoidance of harsh environmental conditions (e.g., nighttime build up of hypoxia or sulfide). Furthermore, the abundance of meiofauna in sediment has been related to flow such that highest sediment densities are found at slack tides (because during times of high flow, some meiofauna are emerged). Even the location of reentry into the sediment by emerged meiofauna is subject to hydrodynamic constraints (e.g., densities may be high in pits and depressions where small particles and meiofauna accumulate).

A number of trends related to body size are apparent in benthic communities. The abundance of macrofauna in estuaries typically ranges from 500 to 10,000 ind/m^2, while biomass ranges from ~5 to 200 g/m^2. For meiofauna, abundances typically range

TABLE 12.5 Biomass and secondary productivity of estuarine consumer communities

Location	Biomass (gC/m²)	Productivity gC/m²/ year)	Main Habitat
Lynher estuary, UK			Intertidal mudflat
	5.43	5.46	Macrofauna
	2.64	20.39	Meiofauna
Baltic Sea	3.39	5.4	Macrofauna
	0.58	2.75	Meiofauna
Grevelingen, Netherlands	10.5	25–29	Estuary average
Forth estuary, Scotland	16.4	14.6	Intertidal upper estuary
	5.1	6.7	Intertidal middle estuary
	1.4	3.6	Intertidal lower estuary
	0.7	0.6	Subtidal upper estuary
Inner Somme estuary, France	5.35	11.1	Fine muddy sand; salinity: 0–30
Swartkops estuary, South Africa	34.7	38.9	Intertidal sands and muds
Berg River estuary, South Africa	9.5	44	Intertidal *Zostera* and mudflat
San Francisco Bay, United States	6.5–12	26.5–50	Intertidal
Long Island Sound, United States	27.3	10.7	Sublittoral average
Southampton Water, United Kingdom	45–95	76–113	Littoral mudflats
Kiel Bight, Germany	13.2	8.95	Sublittoral muds and sands

Source: From Wilson (2002).
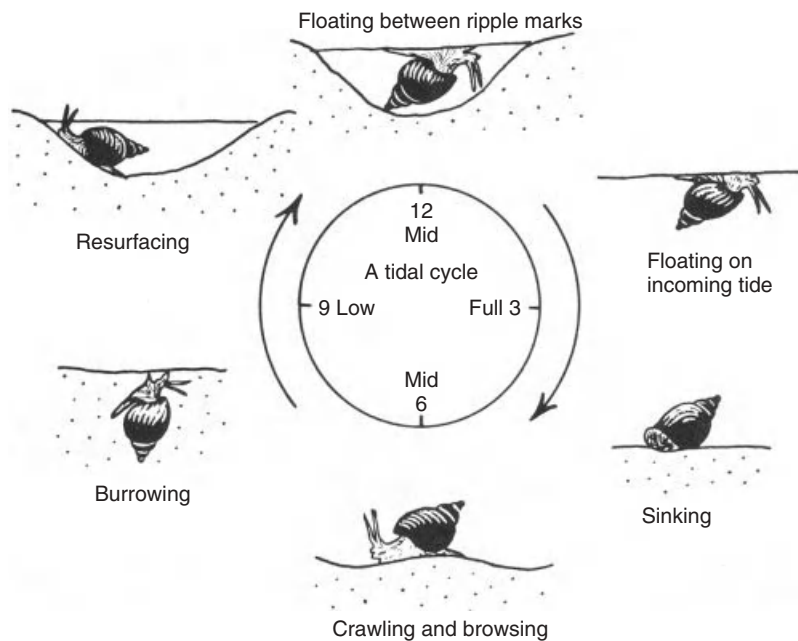
FIGURE 12.6 Flotation of *Hydrobia* on water surface tension and cycle of behavior. *Source:* From Newell (1979).

from 10^5 to 10^7 ind/m² and biomass ranges from 0.5 to 2 g/m² (Table 12.5). Microbenthos have the highest densities but sometimes lower biomass. However, the turnover rate of benthic populations is related to individual size, such that smaller individuals generally have a faster turnover. A similar relationship holds for secondary productivity (Table 12.5). The equations in Table 12.6 were generated empirically from selected but different data sets, but some general principles are apparent. All the relationships are very similar for the range of sizes for which they are valid, but there are notable differences between, for example, the equations for bacteria and for meiofauna. Interestingly, the individual body size exponent of the equations for the fauna in all cases falls within a fairly narrow range, from −0.274 (Brey, 1990) to −0.337 (meiofauna, Schwinghamer et al., 1986), suggesting some underlying physiological constraint, and the

TABLE 12.6 Productivity (*P*) and productivity:biomass ratio (*P*:*B*) as a function of biomass (*B*), body size (*M*, kcal equivalents), and temperature (*T*,°C)

Group	Relationship	References
Bacteria	$P:B = 0.696 * M^{-0.208}$	Schwinghamer et al. (1986)
Meiofauna	$P:B = 0.073 * M^{-0.337}$	Schwinghamer et al. (1986)
Macrofauna	$P:B = 0.525 * M^{-0.304}$	Schwinghamer et al. (1986)
Benthic invertebrates	$P:B = 0.65 * M^{-0.37}$	Banse and Mosher (1980)
Benthic invertebrates	$\log_{10} P = -0.473 + 1.007 * \log_{10} B - 0.274 * \log_{10} M$	Brey (1990)
Benthic invertebrates	$P = 0.0049 * B^{0.80} T^{0.89}$	Edgar (1990)

Source: From Wilson (2004).

different results generated by the equations are due to the different nature of the groups rather than just simple size differences (Table 12.1) among them. Table 12.6 also suggests a temperature, or perhaps latitudinal, effect on productivity (Edgar, 1990), which is higher in warmer waters (Exponent = +0.89).

While clearly the number of individuals (*A*, abundance) and the individual size (*M*, mass) control biomass ($B = A^*M$), secondary productivity is also crucial in evaluating the importance of organisms in estuarine systems. The interaction among these factors can result in almost equal contributions of macrofauna, meiofauna, and microfauna to system productivity (Table 12.7). In turn, productivity is related to the rates of other physiological processes such as respiration, consumption, and N excretion. Some examples of secondary producer biomass and productivity from a range of estuaries are shown in Table 12.5. These data show a remarkable consistency among the systems, with both biomass and productivity values for the estuarine benthic system clustered around 10–20 gC/m^2/ year.

Benthic communities in estuaries are sensitive to environmental change and are often used to help characterize ecosystem health. However, some communities are highly persistent over time. The species diversity of two macrobenthic communities in Dublin Bay, Ireland, over a period of some 20 years illustrates long-term consistency (Fig. 12.7). The number of species in the two communities has remained remarkably consistent over the period, but the balance among species, as evidenced by the Shannon index, an index of species diversity, has changed. For much of the period, the two sites showed remarkably similar trends, namely an increase in Shannon diversity in the early years followed by a decline until the middle of the 1990s, when the two sites diverged (Fig. 12.7b). This divergence was not due to a change in the number of species (Fig. 12.7a) but a change in the numbers of individuals, indicating how the balance between recruitment and mortality affects community structure.

12.5 TROPHIC INTERACTIONS AND ECOLOGICAL ROLE

Benthic communities play significant roles in the flow of energy, in the cycling of nutrients, and in trophic transfer in estuaries. Infauna are known to enhance the rate of decomposition of detritus by several direct or indirect means, including (i) reducing the particle size of detritus by ingestion and passage through the digestive tract, increasing the susceptibility of detritus to microbial attack; (ii) increasing sediment O_2 content by bioturbation, which enhances aerobic decomposition; (iii) grazing on microbes which alters the ratio of senescent to active bacteria, favoring active bacteria; and (iv) mobilizing nutrients. Large benthic animals also increase the flux of nutrients from sediment to overlying water by irrigating burrows and by reducing the compaction of sediments by extensive bioturbation. Rates of nutrient release from sediments are thus increased by benthos, ultimately increasing pelagic productivity. Benthos may also contribute to

TABLE 12.7 Biometrics for macro-, meio-, and microbenthos[a]

Group	Individual Weight (gC)	Biomass (gC/m^2)	*P*:*B* ratio	Productivity (gC/m^2)
Macrobenthos	0.1–100	4.0–200	1:1	5–200
Meiobenthos	0.03×10^{-3}	0.5	10:1	5
Microbenthos	0.1×10^{-6}	0.05	50:1	2.5

[a] 1 gC ≡ 2 g AFDW ≡ 10 g wet weight (excluding shell).
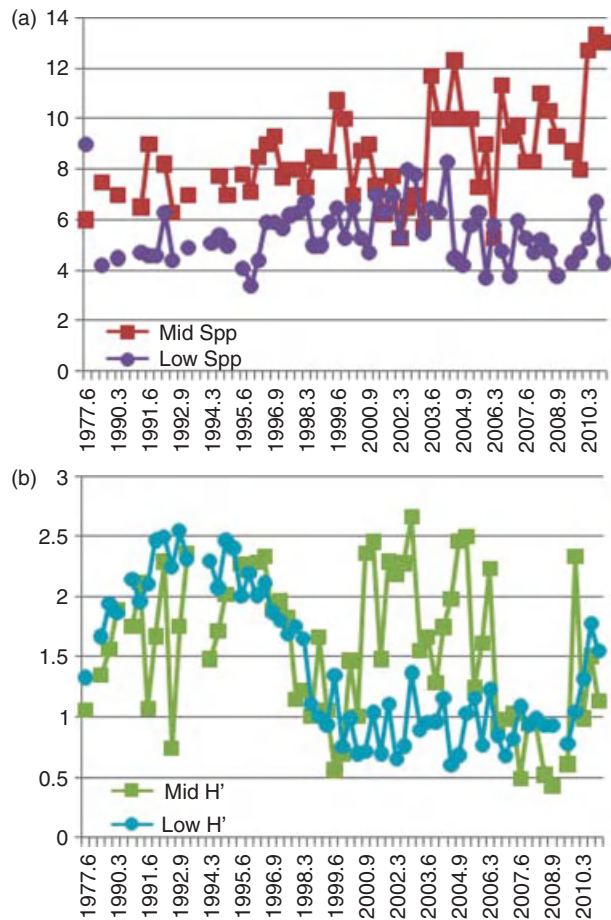
FIGURE 12.7 (a) Number of species and (b) Shannon–Weiner index (H′) at two sites in Dublin Bay, Ireland (Wilson, unpublished data).

the transfer of contaminants from the sediments to the pelagic food chain by trophic transfer.

Another principle role of benthos is to mediate transfer from lower trophic levels, and thus the amounts transferred depend a great deal on the input of energy to the benthos. There is variation in the variety of primary producer inputs to estuarine systems and substantial intersystem variability in the proportional contributions of each (Table 12.8).

These are then linked to feeding types of the primary consumers, thus determining the primary pathways of transfer.

For estuarine systems, in general, there is generally a greater transfer of primary productivity through the benthic system than the water column (Table 12.9). This is one of the driving forces for the importance of benthic food webs in estuaries that contribute to the nursery function for fish and crustaceans, which include important fishery species. But the shallowness and cycle of deposition/resuspension in many systems can blur much of the distinction between surficial sediments and water column suspended particulate matter, and many benthic diatoms, for example, are commonly found in estuarine phytoplankton samples. Also, much of the autochthonous estuarine primary productivity is transferred to higher trophic levels via the decomposer (fungi/bacteria) pathway rather than directly grazed by herbivores, and detritivores may ingest, both selectively and unselectively, the microphytobenthos on the sediment surface; therefore, benthic consumers contribute disproportionately to estuarine energy flow.

On North America's Atlantic coast, the estuarine snail *Littoraria irrorata* first stimulates and then grazes fungi that grow on marsh grass. Experiments have demonstrated a facultative, farming mutualism between *L. irrorata* and the fungi, which also suppresses marsh grass production in which the snail grazing on the grass prepares the substrate for the fungal infection, and thus may exert top-down control of primary production (Silliman and Bertness, 2002).

The imbalance between benthic and planktonic pathways continues to higher levels (Table 12.9), in terms of both primary consumer biomass and productivity. Biomass is a biased measure of comparison, where benthic organisms may be many times larger than their planktonic counterparts, but productivity is similar.

The low diversity in estuaries may also be a factor in the structuring of food webs, which may be only two steps long (e.g., primary production =>

TABLE 12.8 Balance (% of total) of energy inputs from primary producers (phytoplankton, PP; microphytobenthos, MPB; macroalgae; submerged aquatic vegetation, SAV; and saltmarsh) into estuarine systems

Source of Input	PP	MPB	Macroalgae	SAV	Saltmarsh
Grays Harbor, WA	4.3	10.7	8.7	44.2	32.1
North Inlet, SC	12.0	29.0	13.0	0	46.0
Sapelo, GA	7.6	14.4	ns	0	78.0
Ythan, Scotland	15.8	4.9	79.2	0	ns
Dublin Bay, Ireland	1.8	42.6	12.2	<0.1	43.5

Source: From Wilson (2003) and references therein.

TABLE 12.9 Relative importance (biomass, gC/m²; secondary productivity, gC/m²/ year) of water column (zooplankton) and benthic (benthos) pathways in the estuarine environment

Estuary	Zooplankton Biomass	Zooplankton Productivity	Macrobenthos Biomass	Macrobenthos Productivity
Chesapeake Bay, USA	0.39	0.38	5.2	5.5
Apalachee Bay, FL	0.03		1.81	
Ythan, Scotland	0.12	0.83	28.2	68.3
Dublin Bay, Ireland	0.02	0.14	14.9	15.7
Somme, France	0.04	0.24	16.0	9.5

Source: Data from Wilson et al. (2008) and references therein.

benthos > = vertebrate consumer). Since, as a rule of thumb, only about 10% of the energy at one trophic level is transferred to the next, the fewer the transfers, the more of the primary production or allochthonous inputs ends up in the top consumers, including humans. A simple box model for Dublin Bay illustrates these general principles (Fig. 12.8), especially the size of allochthonous inputs relative to primary production, the central role of the benthos as consumers, and short food chains. The largest part of the contribution to estuarine food webs from benthos is from macrofauna. However, meiofauna, especially harpacticoid copepods, also contribute as food for young-of-the-year fish (not shown in Fig. 12.8) and crustaceans. Some species (e.g., flatfish, salmon, and brown shrimp) are heavy feeders on meiofauna consuming thousands per day. These nekton species undergo feeding shifts to larger prey as they grow and the distinction between meiofaunal and macrofaunal feeders is somewhat blurred.

12.6 SUBSTRATE–BENTHIC RELATIONSHIPS

The physical habitat itself can influence what kinds of benthic communities may establish, from hard substrata needed by epifauna for attachment to the soft substrata for infauna. In some cases, the fauna and the substratum are one and the same, where the success of mussels or oysters has reached such proportions as to physically dominate the habitat, turning a soft, muddy substratum into a reef of hard shells. The reef of the Eastern Oyster, *C. virginica*, forms a community of numerous organisms (Fig. 12.8). The dynamics of this process has been discussed in this chapter. Sediment type is frequently related to benthic communities and there is a long history of research relating sediment and benthic communities in estuaries. For example, while many species are found over a wide range of sediment types, most display
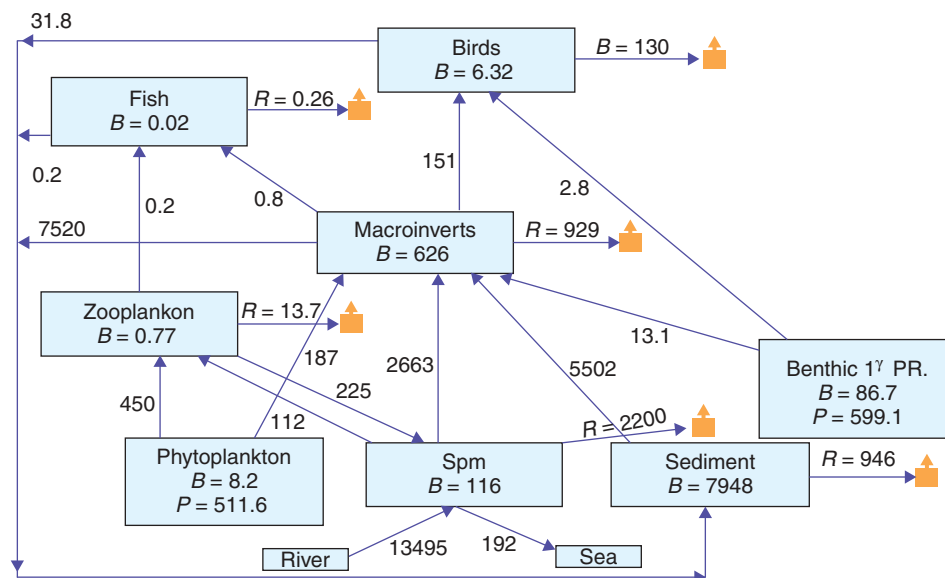
FIGURE 12.8 Simple box model of energy flow through the ecosystem of Dublin Bay, Ireland.
Source: From Wilson et al. (2007).

clear preferences for a much narrower range (e.g., *M. balthica* occur from just below low water almost to the high tide limit in sediments of 0–60% silt). The ability to relate communities and sediment may be due directly to differences in pore spaces and the architecture of the sediment particles or to the strong indirect effect of sediments on chemical gradients within sediments (Snelgrove and Butman, 1994; Fig. 12.9). Sediment type also features prominently in classification systems for estuarine benthic communities such as the EUNIS scheme adopted in Europe by the EU (http://eunis.eea.europa.eu) or the NOAA scheme in the United States (Allee et al., 2000). Sediment type is relatively unchanging at a given location relative to the variability inherent in the water column and often assigned to category (rock, sand, mud, etc.). Furthermore, sediments are often repositories for pollutants, and sediment chemistry is used as an important criterion for risk assessment and environmental health.

Within the sediment itself, the infauna are confronted by steep and varied gradients of physicochemical changes with depth (Fig. 12.9). The actual depth of the redox profile discontinuityRedox Profile Discontinuity (RPD) and the steepness of the gradient are controlled by the rate of movement of oxygen into the sediment and its rate of consumption. In coarse sediments such as sands, with large spaces between the grains, the RPD occurs many tens of centimeters below the surface, while in finer muds, it may be measured in fractions of a millimeter. The availability of oxygen is a major factor controlling the depth distribution of benthos. The deeper macrofauna must maintain a contact with the overlying water either through long, extensible siphons, as in the larger bivalves, or through irrigated burrows. Meiofauna rely on other adaptations to live below the RPD. Some meiofauna live at depth in the oxygenated halo around burrows of large macrofauna, some display body shapes that are longer and/or thinner to enhance diffusion or are long enough to extend into the oxic zone, and some appear to tolerate anaerobic conditions but migrate to the oxygenated surface for gas exchange.

The nature of the substrate is closely linked to hydrographic dynamics (Chapter 2) and in particular by the relationship between water energy (current speed or waves) and sediment particle size; the higher the energy, the larger the particle that may be transported. However, this relationship is not as simple as it may seem (Fig. 12.10) in that slightly more energy is needed to pick up and move a particle once it has been deposited, and in the case of the finest sediments (silts and clays), the electrostatic attraction between

the particles causes them to stick together (hence the term *cohesive sediment*) and thus acts as an increasing barrier to prevent resuspension (Chapter 2).

12.7 HABITAT–BIOTA INTERACTIONS

The biota may themselves play an important role in providing or modifying habitat. Benthic communities are often higher in abundance and species diversity in oyster reefs, seagrass beds, and mangroves compared with nearby nonvegetated areas. Plants especially may improve the environment for consumers by providing food, shelter, and the amelioration of harsh environmental conditions (e.g., plant roots oxygenate sediment). In addition, the complex physical structure of plant communities and reefs baffle water flow, increasing the potential for larval settlement. Plants may serve as substrate for epiphytic algae and shade the seafloor. Therefore, plants in estuaries (e.g., marsh macrophytes and mangroves) have been called *foundation species*, increasing consumer abundance and diversity (Crain & Bertness, 2006).

Suspension and deposit-feeding benthos may also modify the environment-enhancing plants and other biota. Many examples of this ecological engineering have been investigated. Suspension-feeding invertebrates filter large volumes of water in estuaries, removing algae and suspended sediments and transferring large numbers of fecal pellets to the sediment. Fecal pellets are rich in nutrients that alter nutrient dynamics by enriching sediment nutrient content and plant growth. Deposit-feeding and large burrowing invertebrates are important bioturbators that increase the depth of oxygen penetration into the sediment. Experimental studies have shown that fiddler crabs enhance *Spartina alterniflora* production and flowering at least partly by stimulating mycorrhizal associations on plant roots as a by-product of burrowing that aerates the soil (Daleo et al., 2007).

12.8 OXYGEN/HYPOXIA

Many factors influence oxygen availability to benthos and the faunal response to reduced oxygen concentrations. Epifauna experience variation in oxygen availability along the subtidal/intertidal/supratidal gradient driven both by the amount of time of exposure to air (when atmospheric oxygen is available) and by the mixing and movement of the overlying water. Subtidal sediment oxygen concentrations
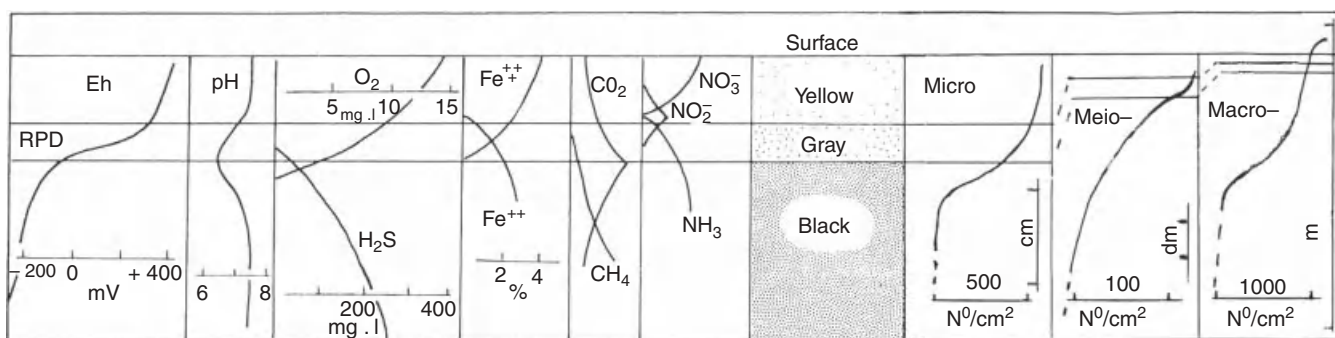
FIGURE 12.9 Chemical and biological gradients in the sediment. *Source:* After Fenchel and Reidl (1970).
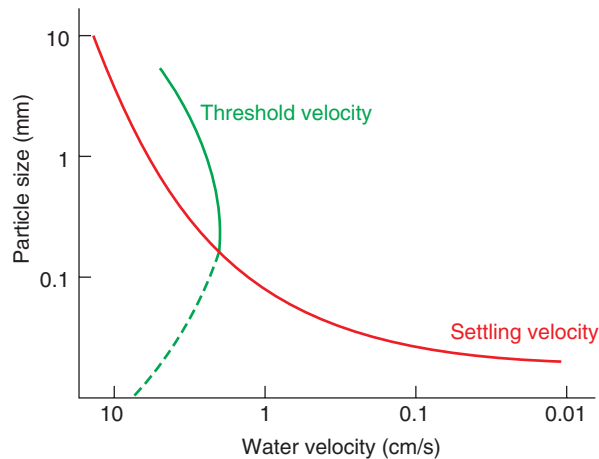
FIGURE 12.10 Sediment particle size and water energy. *Source:* From Wilson (1988).

FIGURE 12.11 Oxygen sag in the Liffey estuary: DO level and chlorophyll concentration in the water with time. Courtesy T. O'Higgins, Dublin Corporation.

vary as a function of the concentration in the overlying water, photosynthesis by benthic algae, and oxygen consumption by microbes and the infauna themselves.

Variation in sediment oxygen concentrations in estuaries may be diurnal, associated with tidal currents, seasonal, or highly variable. In some European estuaries, a combination of neap tides, high temperatures, decaying phytoplankton blooms, and high benthic density can arise on decadal scales, causing low oxygen conditions and benthic mortality. Estuaries often have a tendency toward low oxygen concentrations. An often-noted characteristic of estuarine systems is the ''oxygen sag'' in which oxygen saturations may permanently be well below full saturation in some reaches of an estuary (Fig. 12.11). A principal factor in the oxygen sag is the turbidity maximum, where high concentrations of suspended particulate matter not only contribute to the sag through the respiration of the associated microbes but also restrict light that might otherwise increase photosynthesis and reoxygenation. This phenomenon may be particularly pronounced when scouring is sufficient to resuspend some centimeters of the bottom sediments, including those below the RPD (Fig. 12.9), in which oxygen is used up in the chemical reactions as the reduced compounds are reoxidized.

Benthic infaunal responses to hypoxia, defined as oxygen levels below 2 ml/l, typically involve avoidance or mortality of large-bodied species and elevated abundances of enrichment opportunists. Responses of benthos to hypoxia depend on the duration, predictability, and intensity of oxygen depletion. Calcareous foraminiferans and nematodes are particularly tolerant of low oxygen concentrations and
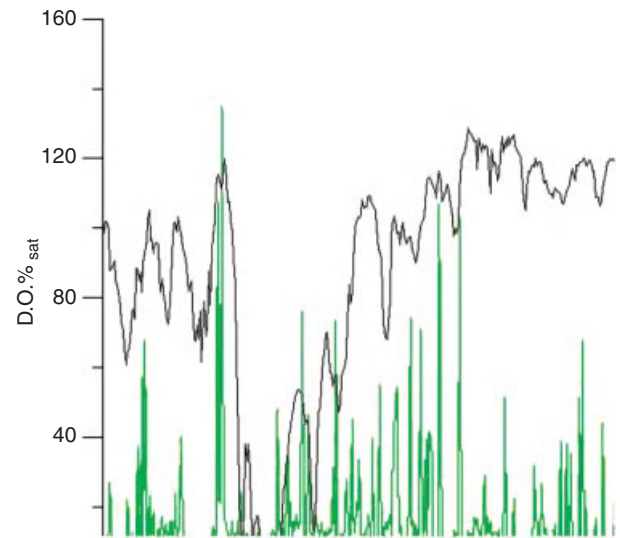
may attain high densities and dominance. When oxygen is sufficient to support metazoans, small, soft-bodied invertebrates (typically annelids), often with short generation times and elaborate branchial structures, predominate. Crustaceans and echinoderms are typically more sensitive to hypoxia and have higher oxygen thresholds than annelids, mollusks, and cnidarians. Within a species, early life stages may be more subject to oxygen stress than older life stages. Hypoxia alters both the structure and function of benthic communities, but effects may differ with regional hypoxia history. For example, infauna living on mudflats are likely to be tolerant to hypoxia on the timescale of many hours as an adaptation to living on mudflats, which frequently experience nighttime hypoxia.

Under both natural and eutrophication-caused hypoxia, there is loss of species diversity through attrition of intolerant species and the community shows elevated dominance, as well as reductions in individual body size. These shifts in species composition and diversity yield altered trophic structure, energy flow pathways, and corresponding ecosystem services such as production, organic matter cycling, and organic C burial. Hypoxia, for example, may alter the fate of energy in that more energy is used by microbes and less is used by animals under conditions of hypoxia (Diaz and Rosenberg, 2008).

Hypoxia also provides a good example of the interaction between biological and physicochemical factors in estuaries. In hypoxic conditions, many benthic species will leave the sediment (and may

also become sluggish, often to the point of coma before actual death) that then leaves them vulnerable to nektonic predators. Recent work has shown in these conditions that the predation on the benthos is increased and has a significant effect on the structuring and function of the benthic system.

12.9 BENTHIC RECRUITMENT AND THE ABUNDANCE OF ADULTS

The adjacent sea can be a source of sediments, nutrients, salinity, and oxygen as well as a pathway for active and passive migration of juvenile and larval forms. Much of the estuarine benthos is of marine origin and the majority of the organisms retain many of the typical features, including planktonic larvae. The planktonic phase is a vital mechanism through which benthic species are dispersed, but in the dynamic conditions in many estuaries, there is a high risk that the larvae may be flushed from the system. Some species, such as *N. diversicolor*, have evolved a modified planktonic phase in which not only is the time spent in the plankton reduced in comparison to similar fully marine species but the larvae also stay close to the seafloor. In this way, they can take advantage of the hydrographical structuring both in terms of higher salinity and up-estuary movement of the salt wedge.

Another classic example of biological exploitation of estuarine hydrography is illustrated by the blue crab, *Callinectes sapidus* (for an example from the Chesapeake, see Bell et al., 2003). Adults live in mid-estuary, the females migrate to the coast (near full-strength salinities) to spawn, the larvae develop through the various stages in the coastal waters, and the megalopae drop down in the water column into the salt wedge to be transported back into the estuary where they molt into juveniles and continue up-estuary to their adult habitat.

In general, the tolerances of larvae are narrower than those of the adults, such that the adults may survive in conditions of salinity (or other stressor or combinations of stressors) where the larvae would not. Under these circumstances, successful recruitment and colonization is dependent either on mechanisms such as that for the blue crab or on a temporary amelioration of conditions coinciding with the availability of the larvae in the water column. As a consequence, many estuarine populations show an irregular cycle of abundance, where a good recruitment year may be followed by several poor years.

As mentioned above, estuarine populations are subject to considerable fluctuations, often controlled by stochastic processes determining recruitment success. However, not all control is exerted by physicochemical parameters. Figure 12.12 shows a model of cyclic fluctuations in cockle (*Cerastoderma edule*) populations in which both internal and external biological factors modify density following initial settlement. Successful settlement leads to a rapid increase in numbers. This, coupled with growth of individuals, induces increasing intraspecific competition, which acts to restrict further growth in the population. As the population ages, mortality increases in older individuals, and there is poor recruitment due to the negative effect of high adult densities on the success of recent recruits, leading to a fall in the numbers.

A cycle of abundance alternately dominated by *C. edule* and a tube-building spionid polychaete
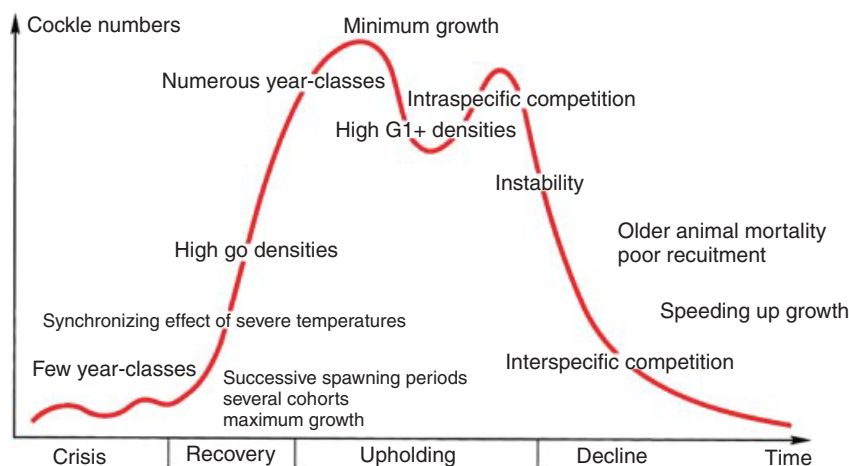
FIGURE 12.12 Population cycles in the bivalve *C. edule. Source:* From Ducrotoy et al. (1991).

(*Pygosio elegans*) has also been described, with each being able to partially exclude the other by virtue of exceptional densities at the height of the cycle (Fig. 12.13). *P. elegans* is an excellent opportunist species, able to colonize when *C. edule* numbers are low. The tubes of *P. elegans* stabilize the sediment and accelerate accretion, causing the shore level to rise and rendering the habitat less suitable for *C. edule*. *C. edule* reestablishes only when the *P. elegans* colonies have grown to such an extent that the level of the substratum has been significantly raised and the animals are subject to high tide levels of temperature and desiccation. When the worms die off, their tubes break up and the sand bank erodes down to its original level, leaving a now-vacant space for the cockles.

A similar cycle has been shown in the growth and maturation of mussel (*M. edulis*) beds (Fig. 12.14) and oyster reefs on mudflats. Mussels adhere to hard substrates by their byssus threads, which not only offer a strong attachment but can also be used for positioning and local movement by detaching and reattaching. As epifauna, they require something solid to first attach. This first attachment can be a stone or a shell to which the byssus is attached. If the individual survives, then its shell in turn offers hard substratum for future settlers, whose byssus threads act to bind together the clump along with anything else they may be able to attach to. Once the clump reaches a certain size, then its own weight confers stability and prevents it from being displaced or otherwise washed away. Successive waves of settlers then increase both the size and height of the mussel bed, since not only do the settlers favor the top of the clump but the top
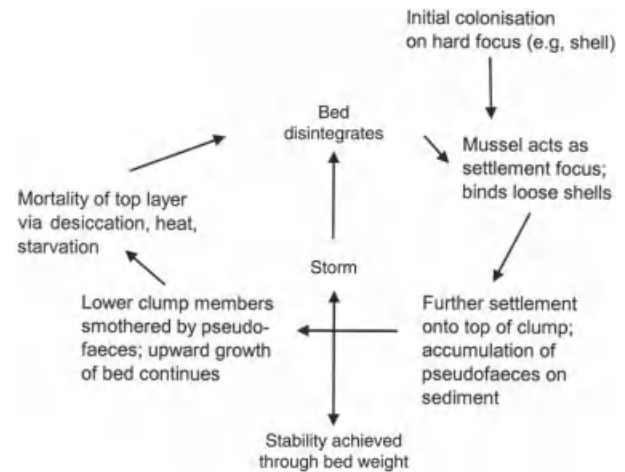
FIGURE 12.14 Diagrammatic representation of the cycle of mussel-bed buildup and dieback.

position also confers a double advantage. Those at the top have better access to both the food, since mussels are suspensivores, and oxygen in the water column, while the feces and pseudofeces, which fall into the clump, greatly accelerate the tendency toward anoxia underneath. Oyster reefs undergo similar dynamics and can be created if hard substrates, including oyster shell (artificial ones are called *Oyster cultch*), are placed on the muddy seafloor. Mature reefs of *C. virginica* reach into the intertidal zone on the east coast of North America, and reef height is important for stability. Reefs that are too short to extend above the near-bottom hypoxic zone are less productive. Overfishing the oyster reef can reduce reef height and threaten reef productivity.

The model of irregular recruitment into estuarine benthic populations, and the effects on population growth and production, was set out by the work of Hughes on the bivalve *Scrobicularia plana* (Hughes, 1970). The classic pattern that emerged was of a sporadic and even stochastic frequency and intensity of settlement, in which a single good recruitment is marked by a peak in abundance, which could be followed over the subsequent decade, when population dynamics were largely governed by the performance of that year class. In such circumstances, benthic community composition becomes a function of the regularity of recruitment and the longevity of the component species.

There is some evidence of density-dependent regulation of suspensivore populations. Recruitment of juvenile cockles (*C. edule*) is negatively affected by high densities of the adults, although whether this is due to the adults actually taking the larvae themselves (possible, but unlikely in numbers given their size) or simply that the adults are removing much of the
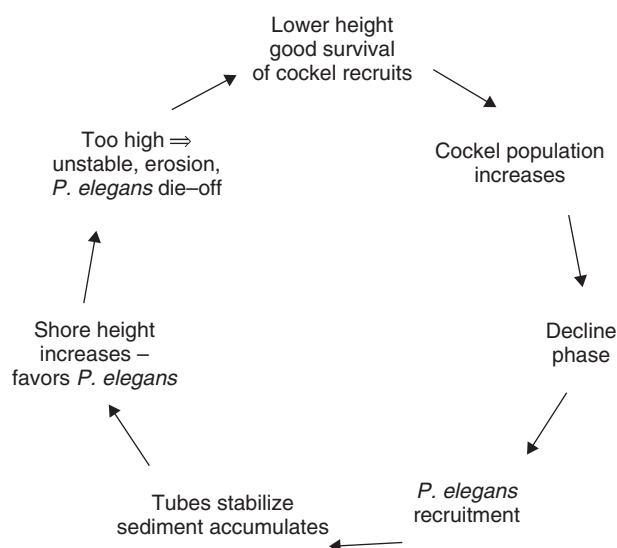
FIGURE 12.13 Model of interactions between *C. edule* and *P. elegans*.

food from the water column and thus decreasing the amount available for larvae is unclear. Such a negative feedback mechanism should, in accordance with the theory that biological controls act in a density-dependent manner, result in a dampening of the population fluctuations, but since this appears to rarely be the case (Table 12.5), the nondensity-dependent factors (e.g., physicochemical factors and external influences) must be presumed the more important. On a regional basis, temperature has been shown to exert an influence on cockle recruitment, although the influence is not straightforward. Both unusually low and unusually high temperatures affect recruitment, but the degree of influence and the mechanism (e.g., condition of parents and timing) through which recruitment is affected varies with location, as does the impact of such temperature anomalies.

12.10 PREDATION TOP-DOWN AND BOTTOM-UP CONTROL

Benthic consumers are key intermediates in estuarine systems because a large fraction of the flow of energy is associated with sediments both on the bottom and in suspension and channeled through infauna and/or epifauna. Top-down trophic cascades occur when predators in a food web suppress the abundance of their prey, thereby releasing the next lower trophic level from predation (i.e., the top-down effect spans two or more trophic levels such that removing top predators has indirect effects on lower trophic levels). Estuarine benthos may experience top-down effects; suites of predators (including invertebrates, fishes, and birds) exert influence on benthic populations, and large predators in many estuaries have been diminished by overfishing or other human activities. However, the potential for trophic cascades appears to differ for infauna and epifauna. For infauna, predator exclusion studies suggest that benthic animals increase in abundance in the absence of predation but without a change in species diversity (no species competitively excludes others). But this top-down control does not extend to the prey of infauna, that is, benthic microalgae do not decrease in abundance when infauna increase. Infauna interact weakly with benthic microalgae, perhaps because the diet of infauna is diverse (Johnson and Fleeger, 2009). However, epifauna may be important intermediates in a significant top-down trophic cascade, involving *S. alterniflora* in which top predators (such as blue crabs) indirectly influence primary producers via herbivory by *L. irrorata*. Similar conclusions of the importance of trophic

cascades have been reached in sea grass communities and their epiphytes in estuaries (Heck & Valentine, 2007).

The alternative to top-down control is that benthic systems are also controlled by bottom-up factors such as food or nutrient (N and P) loading. Experimental evidence suggests that food quality of the sediment may limit infaunal populations (Cheng et al., 1993) and that adding food (detritus) leads to increases in population density, especially for deposit-feeding species. However, infauna may respond to increased food quality by increasing body size or production without increases in population density. Questions of bottom-up control are relevant because many estuaries have experienced increases in nutrient loading, thus increasing primary production, and it is important to know how benthic populations respond and if they feedback to primary producers. The relative importance of top-down and bottom-up forces to benthic fauna is also of interest but has been difficult to address because large-scale manipulative experiments are difficult to conduct and are rare in estuaries (Deegan et al., 2007). Interactions between top-down and bottom-up forces appear to be rare (Posey et al., 2002) but are potentially important because human activities frequently reduce top predators and simultaneously increase nutrient loadings.

The shorecrab (*Carcinus maenas*) provides a classic example of predator/prey interaction in its feeding on *M. edulis*. Experiments have demonstrated that not only is there a strong link between the size of crab and the size of mussel taken, but that the crab strategy is one of optimal foraging. The larger the mussel that is eaten, the greater the reward (amount of energy) to the crab. However, the larger the mussel, the more time and energy it takes to open it, and so the optimum strategy is one of minimizing the costs, while maximizing the return with the result that there is an optimum size of prey to be taken. Smaller mussels can be taken if the optimum size is scarce, but when the mussel reaches a certain size, the shell is too thick and solid to be cracked by the crabs and they then become invulnerable to crab predation. The influence of this is clearly shown in Figure 12.15, as it is for the other predators in terms of the age structure of the shellfish prey population.

12.11 HUMAN IMPACTS ON ESTUARINE BENTHOS

There is a long history of human exploitation of the estuarine benthos. The abundance of many
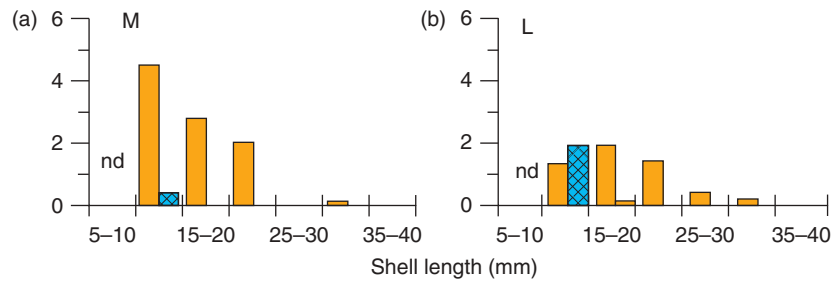
FIGURE 12.15 Optimal foraging and size selection of mussels (solid bars) and cockles (hatched bars) by large (L) and medium (M) crabs. Vertical axis is size of crab in centimeter. *Source:* From Mascaro and Seed (2001).

estuarine shellfish populations has long been exploited and indeed overexploited. Table 12.10 lists some of the major estuarine species taken and also the very considerable quantities, which has not been without impact on the estuarine system.

The first recorded commercial lease of an oyster bed is documented from 1705 in Dublin Bay, Ireland, for which the fee for one bed alone was 10,000 oysters annually to be paid to the Mayor plus 1000 a year to each of the Sheriffs. At present, almost no trace remains of the extensive oyster beds in Dublin Bay, and while pollution may have played a part, such a high level of exploitation cannot have been sustainable. Interestingly enough, the Dublin Bay cockles

were also widely exploited, with some 6000 gallons (about 100 tons) taken annually, at least until their collection was forbidden in 1908 on public health grounds, yet their populations still seem to be about the same today as formerly.

The Eastern oyster, *C. virginica*, in the Chesapeake Bay has also suffered as a result of exploitation and pollution. It was estimated that at the time of the heyday of the fishery at the end of the nineteenth century, over 300 million bushels (just under a million tons) of oysters were taken in the state of Maryland alone, and the standing stock of oysters was by itself capable of removing almost 80% of the phytoplankton of the system (Newell, 1988). The decline of the oyster

TABLE 12.10 Annual harvest (1999 catch, $\times 10^3$ tonnes) and salinity tolerance of estuarine consumers with comments on status of stocks

Species	Comments	Salinity Range	1999 Catch
Mytilus edulis	Northern Europe, Cultured widely: hybridizes with *M. galloprovincialis*	3–35	122
Mytilus galloprovincialis	As *M. edulis*; southern Europe, Mediterranean, and Black sea	10–35	56
Perna viridis	As with other *Perna* species increasingly fished and cultured	18–33	22
Mussels	Global harvest		1689
Callinectes sapidus	Chesapeake Bay–blue crab, no. 1 seafood, larval salinity tolerance >20	0–35	105
Crangon crangon	Local fisheries, not cultured	5–35	37
Penaeus monodon	Widely cultivated	10–35	144
Crab, prawn, shrimp	Global harvest		4126
Crassostrea virginica	Chesapeake Bay harvests, much reduced	5–30	146
Crassostrea gigas	Most popular species for worldwide culture, spawning temperature restricted in NorthEurope	8–36	12
Ostrea edulis	Beds much reduced and threatened by diseases	24–35	2
Oysters	Global harvest		3869
Cerastoderma edule	Laborious to collect: now mechanized methods (with environmental conflicts)	15–35	70
Nereis virens	Fishing bait, now small-scale culture	15–35	0.3[a]
Glycera dibranchiata	Fishing bait, restrictions, and quotas apply	12–47	0.3[a]

[a]Data for State of Maine only: peak tonnage (1980–1999) quoted.

stocks to a fraction of their former level, and the resulting decline in the control on the system exerted by the oyster, was suggested as a causative factor in the change in the system, and in particular the abundance of ctenophores and sea nettles.

A confounding factor in the decline of *C. virginica* in the Chesapeake has been disease, especially the unicellular parasite MSX, and serious consideration has been given to replace the native oyster with its Japanese equivalent. The latter is resistant to MSX, and, by restoring oyster populations back toward their historical levels, they would bring the system back to what it had been. However, this plan has been vigorously opposed, as the history of introductions of nonnative species is littered with unintended and usually harmful consequences. The European flat oyster, *Ostrea edulis*, is a good case in point. As their stocks diminished throughout Europe (see example above of Dublin Bay), they were replaced first by *C. virginica*, and then by *C. gigas*, not least because these introduced species grew faster and were ready for

market in 2 years, as opposed to the 3 or 4 years required by *O. edulis*. However, these introductions brought with them (among others) the slipper limpet *Crepidula fornicata*, which is a feeding competitor that also overgrows the oysters and covers them with feces; the oyster drill *Urosalpinx cinerea*, which is a predator; and the oyster wasting disease *Bonamia ostreae*—an intracellular parasite. It is the last of these which is having the greatest effect on the remaining *O. edulis* beds, and a great deal of effort, and regulation, is being expended to control and restrict any further expansion of the condition into unaffected areas.

In larger estuaries, trawling for fish and dredging of shellfish have major physical, chemical, and biological impacts, as does the dredging of channels for shipping. Table 12.11 lists some of the major impacts and consequences for the benthos.

Pearson and Rosenberg in 1978 developed the classic model of the effects of stress/pollution on the benthos (Fig. 12.16). After a disturbance, opportunist benthic species are the first to colonize the sediments

TABLE 12.11 Anthropogenic activities, especially fisheries, mode of action and degree of impact on the estuarine consumers

Human Activity	Mode of Action	Relative Impact
Reclamation, infill, etc.	Direct or indirect removal of habitat	High
System management	Bias toward certain selected taxa	High
Pollution/contamination	Death, avoidance, lifting of limitations	High
Fishing	Removal of species	High
Mechanized fishing	Habitat alteration/modification	Low (in estuaries)
Aquaculture	Enhancement of selected species	Medium
Aquaculture	Cointroduction of exotics	High
Aquaculture	Selective breeding	High to low, depending on species
Freshwater withdrawal	Salinity changes	High

Zone	Normal	Transitory		Polluted	Grossly polluted
Typical macrofauna dominant	Nucula Amphiura Torobelldes Rhodine Echinocardium Nephrops	Labidoplax Corbula Goniada Thyasira Pholoe	Chaetozone Anaitides Poctinaria Myriocheie Ophiodromus	Capitella Scoloiepis	No macrofauna Surface covered By fiber 'blanket'
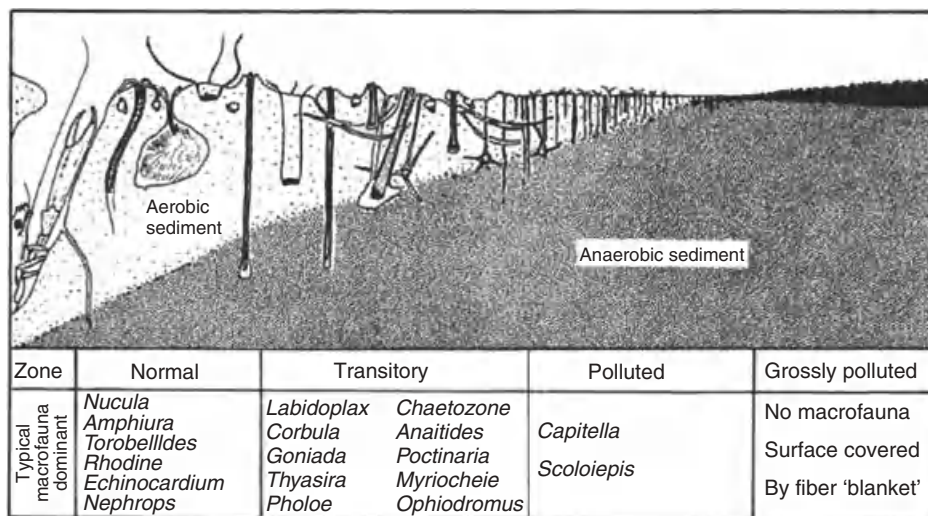
FIGURE 12.16 Benthic community response to pollution. *Source:* From Pearson and Rosenberg (1978).

as the situation improves, followed by increasing numbers of other species, until, as control shifts from physicochemical control to biological control, superior competitors with poor colonizing abilities come to dominate. This model works well for estuarine benthos for a number of stressors, including organic pollution, nutrient pollution, hypoxia, and toxins both in time after a disturbance and in distance from a point source. However, since estuaries tend toward disturbance and physicochemical control, the benthic communities may never actually attain the "normal" status as defined in the model. Pearson and Rosenberg (1978) produced a list of opportunistic benthic species, many of which are found in unpolluted estuaries (Table 12.12). In a way, it is not surprising that

species that are adapted to respond to the natural stresses and the variability of the estuarine system have the capacity to respond to anthropogenic contamination. However, as with all stresses, the effects cannot be taken in isolation, and while estuarine benthos as a group may be relatively resistant overall, the impact of a contaminant is often much greater when salinity or other stress is added.

In the same way that the paucity of species in estuaries makes the use of diversity indices (e.g., Shannon index) questionable as reliable indicators of health or status, the opportunistic tendencies and the general stress resistance of the benthic community affects their value as indicators of pollution. Table 12.12 shows the classifications in two recent pollution indices along

TABLE 12.12 Macrobenthos in estuaries, as grouped by Borja et al. (2004), associated by Rosenberg et al. (2004) with impoverished communities (ES50), and linked by Pearson and Rosenberg (1978) to pollution

Taxon/Species	Borja et al. (2000) Group	Rosenberg et al. (2004) ES50	Pearson and Rosenberg (1978) List	Estuarine Occurrence
Capitella spp.	V	1.5	Yes	Outer
Capitelloides giardii	V	—		Outer
Oligochaeta	V	7.8	Yes	Yes
Audouinia tentaculata	IV	—	Yes	Outer
Cirratulus cirratus	IV	10.3		Outer
Polydora spp.	IV	4.75	Yes	Outer
Prionospio spp.	IV	11.6	Yes	Outer
Corbula gibba	III	4.7		No
Carcinus maenas	III	6.8		Yes
Corophium volutator	III	9.9		Yes
Cerastoderma edule	III	6.1		Middle
Cerastoderma lamarcki	III	—		Yes
Crassostrea angulata	III	—		Yes
Heteromastus filiformis	III	9.7	Yes	Middle
Hydrobia ulvae	III	2.6	Yes	Yes
Nereis diversicolor	III	—	Yes	Yes
Spio filicornis	III	13.1		Outer
Scrobicularia plana	III	—		Yes
Scolelepis spp.	III	13.4	Yes	Outer
Mytilus edulis	III	5.1	Yes	Yes
Corbula gibba	III	4.7	Yes	No
Eteone longa	II	5.0		Middle
Abra alba	II	4.0		No
Glycera rouxii	II	11.5		Middle
Mya arenaria	II	5.8	Yes	Yes
Nephthys hombergii	II	6.9	Yes	Middle
Pleuronectidae	II	—		Yes
Ophiura albida	II	9.4		No
Eteone longa	II	5.0	Yes	Middle
Crangon crangon	I	7.2		Yes
Amphiura filiformis	I	9.5		No
Gammarus sp.	I	—		Yes
Liocarcinus depurator	I	5.7		Outer
Macoma balthica	I	5.8	Yes	Yes
Scoloplos armiger	I	7.1	Yes	Middle

with Pearson and Rosenberg's (1978) listing in relation to their occurrence in estuaries. The difficulty in applying either of the indices in estuaries, with many of the typical, indeed characteristic estuarine species assigned to group III (Borza et al., 2000), is indicative of moderate pollution. Consequently, true estuarine indices based on the consumer community are scarce. At one end of the spectrum is the very simple biological quality index of Jeffrey et al. (1985; Fig. 12.17), which defines diversity on a comparative scale against that expected in estuaries, with added criteria based on size and number of year classes. But even this can yield false positives under highly hydrodynamic conditions or in areas stressed by salinity variation or other factors. At the other end of the spectrum is the benthic index of biological integrity (B-IBI) of Weisberg et al. (1997) for Chesapeake Bay based on a very extensive set of databases available for the Chesapeake. This index divides the system into seven different habitats on the basis of salinity and substrate in which 17 different metrics are tested for deviation from reference values. While this successfully classifies polluted sites, the efficiency is less in lower salinity categories.

Many estuarine sediments serve as long-term sinks for toxic chemicals in a variety of classes, including heavy metals, hydrocarbons, herbicides, pesticides, and endocrine disruptors. Sediment quality in many estuaries is often degraded because of the presence of these toxins (Long, 2000), and pollutants affect benthic communities in predictable ways in estuaries. Generally, studies have shown that crustaceans and

echinoderms are intolerant of most kinds of sediment contamination and that small-bodied deposit feeders, that is, annelids and nematodes, are most tolerant. Tolerance to contaminants may differ greatly, and some species are very sensitive, while others may be quite tolerant. As a result, pollution may bring about community change due to indirect effects, in which tolerant species change in abundance because competitors, predators, or prey are affected by pollutants (Fleeger et al., 2003).

12.12 SAMPLING

Field sampling of the estuarine benthos is often decided on pragmatic grounds, but there are some general principles that can be applied. In practice, most work on the estuarine benthos is done using quantitative sampling (e.g., the number of individuals per unit area is estimated per m^{-2} or cm^{-2} depending on size), as this gives the maximum amount of information about the makeup of the community. However, this requires time-consuming and expensive field work, laboratory sorting, analysis, and identification. Variation among replicates may be high, necessitating a large number of samples and increasing sampling costs. For true quantitative sampling, sampling methods are those that take a precise area or volume. In practice, the first of the two methods listed (Table 12.13, dredge and net) are at best roughly quantitative and are dependent on 100% of the calculated area or volume being passed through the sampler.

Quantitative sampling with corers or grab samplers is most common. Grabs are available in a variety of configurations and sizes, from 0.01 m^2 for hand-operated units to 0.2 m^2 (or even larger in some cases) for vessels equipped with a winch: 0.1 m^2 is probably the most common. The size of the grab describes the area of its open mouth as it lands on the sediment, while the depth of the sample is a factor of the weight of the grab (up to 0.25 ton on occasion!) and the softness of the sediment. The operation of the grab results in an uneven ''bite'' of the sediment, so that the shape of the bite taken is not a regular rectangle but can be a semicircle or indeed any shape at all. Consequently, organisms at different depths in the sediment may not be equally represented, and a corer may be preferred. Box corers take large volumes of sediment and are often subsampled either as the corer enters the sediment or on ship. Handheld corers using SCUBA techniques offer a precision of sampling not attainable by other means. SCUBA, while increasing
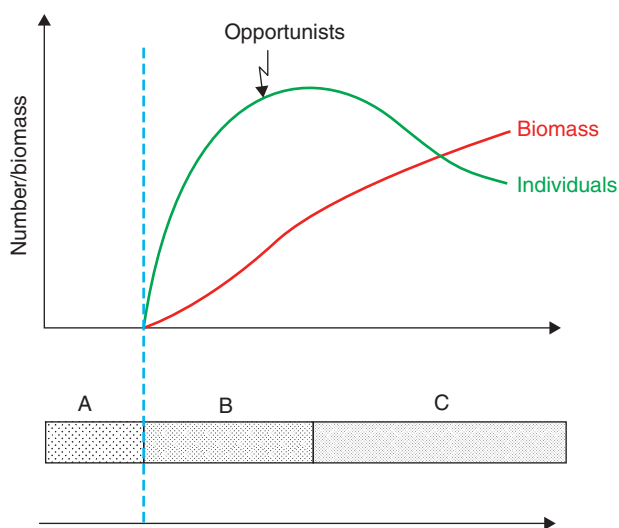
FIGURE 12.17 Biological quality index categories (A, B, and C) along pollution gradient. Pollution decreases from A to C. *Source:* Adapted from Wilson (1988).

TABLE 12.13 Sampling types, sampling level, and equipment with comments

Level	Method/Equipment	Comments
Presence/Absence	All/any	Useful for species lists; some biodiversity, habitat, or biome classifications
Qualitative	Visual, spade, dredge	Rough estimates of abundance/cover. Can be assigned rankings with standard scales
Quantitative	Dredge	Roughly quantitative mouth * length of tow *or* volume retained
	Plankton net epibenthic sled	Roughly quantitative: mouth * length of tow
	Grab	Area defined *but* depth/shape of bite depends on sediment hardness. Control by volume check
	Corer	Area and shape controlled: penetration can be limited in hard sediments
	Hand core (SCUBA)	Can be accurately placed; fine control over sampling
	Camera, video	Useful for epibenthos: stereo > = size, biomass; nondestructive sampling
	SPI, REMOTS	Sediment profile imagery—limited biotic data
	Multibeam, sidescan sonar	Discriminates habitat features and larger assemblages (e.g., oyster reefs)

in popularity, is less used in estuaries than in open coastal waters, not so much on account of the depth limitation but because of other difficulties, notably current speeds, visibility, and microbial pollution.

Imaging (e.g., based on photographs or sonar) methods are gaining popularity for ease and speed of reconnaissance. The list in Table 12.13 details some of these, but the important proviso for all is that they are only as good as the ground truthing on which their interpretation is based, and the recommendation is that they should be used as guides for further investigation rather than be accepted uncritically. However, it should be noted that these methods are being refined and that advances in digital image recognition software (camera and video) and in sonar and multibeam signal processing are making major improvements in their accuracy.

The number of samples to be taken depends on the density of the species sought and can be readily estimated from previous work or a preliminary sampling. When the level of accuracy is established (20% is considered adequate for most ecological work), the number of samples may be calculated according to Elliott's (1971) index of precision (D). This index is based on the results of previous samplings, where D

equals the standard error divided by the arithmetic mean. Thus, the number of samples needed (n) is equal to $1/(mean) * (D)$.

This can be applied to whatever level of precision is required, but note that a doubling of the precision level quadruples the number of samples required. For example, at a 20% level of precision, 25 samples are needed if the average number of individuals per sample is 1, 5 samples are needed if the average is 5, but only 1 sample is needed for an average of 25 (and over). At the 10% level, the numbers of samples required are 100, 20, and 4, respectively 12.

12.13 SUMMARY

Benthic consumers play a pivotal role in estuarine ecosystems. They process primary productivity of the system and inputs from sea and river with such success that they can attain biomasses equal to any other ecosystem on earth. Yet, this success is not without penalty, in that they are at the mercy of a harsh and unpredictable environment, to which all aspects of their biology must attune. The most successful are the permanent residents, while those

of lesser aptitude are confined to the outer (and inner) fringes.

Humans profit greatly from benthic consumers in estuaries, by directly consuming them and by consuming fish and birds that depend on benthic resources. Increasingly, humans are acknowledging the ecological services, especially in support of nutrient regulation and fisheries production, provided by estuarine benthos that will be subject to future pressures from increasing population growth, urbanization, and climate change.

Yet benthic organisms also offer unparalleled opportunities for understanding system function and dynamics. The strength of the drivers—particularly salinity—of the benthic environment should be easier to explain, understand, and model than most, even if they still pose major challenges.

There have been major advances in our understanding of the estuarine benthos and their communities since the first edition of this book, which brought together for the first time many of the fundamentals. The latter have not changed, nor hopefully will the knowledge set out here, but it will serve in its turn as a foundation to take science on to the next level.

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ESTUARINE NEKTON

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13.1 INTRODUCTION

Those who study estuarine nekton are impressed with the adaptations of individual fishes and whole fish communities to existence in an estuary. Estuarine ecosystems are physiologically demanding, relatively unpredictable, and in many ways inhospitable environments. Yet, as a rule, they teem with *nekton* (here defined as *free-swimming consumers*). Although free-swimming consumers include squids, octopii, portunid crabs, peneid shrimps, reptiles, and mammals such as dolphins, seals, and sea lions, fishes constitute the preponderance of estuarine nekton species, and they generally comprise the highest number of individuals and biomass (Yáñez-Arancibia, 1985).

Small larval and juvenile forms (e.g., of fish and crustaceans) are especially abundant, despite their seeming fragility and complex life cycles. The presence of large numbers of juveniles in estuaries is believed to be dependent on two primary factors, the relative importance of which is still debated: (i) Estuaries are regions of high primary and secondary productivity, thus providing elevated food resources for fast growing juveniles and (2) estuaries comprise numerous habitat types that undoubtedly provide small fishes and invertebrates refuge from predators that use estuaries as feeding grounds (Yáñez-Arancibia et al., 1994; Able, 2005; Baltz and Yáñez-Arancibia, 2011). The evidence for estuaries as juvenile habitat is well documented from South Africa (e.g., Whitfield, 1998); Australia (e.g., Potter et al., 1990; Blaber, 2000); the United States (e.g., McHugh, 1967; Ray, 1997; Ray et al., 1997; Able and Fahay, 1998); temperate South America (Chao et al., 1982); tropical estuaries in the Philippines, Colombia, Venezuela, Brazil, and Mexico (e.g., Yañez-Arancibia, 1985; Longhurst and Pauly, 1987; Blaber, 2000); and Europe (Elliott and Hemingway, 2002). As such, estuaries are often referred to as *nursery areas*, a role that is considered by many to be the most important function of these ecosystems to nekton and fisheries (Pauly and Yáñez-Arancibia, 1994).

Whatever physiological and behavioral cost that the nekton pays for living in estuaries appears to be compensated for by the higher survivability of juveniles in estuaries. In many of the world's oceans, high primary and secondary productivity is concentrated in relatively shallow waters on continental shelves and in estuarine basins that receive river discharge, which creates coastal vegetated habitats and biogenic reefs, thus facilitating use by nekton in temperate, subtropical, and tropical latitudes.

Besides the two factors mentioned above, some fishes use estuaries as migration routes between adult habitats and their spawning grounds. Collectively, these fishes are referred to as *diadromus* but are further divided into two groups: (i) anadromous and (ii) catadromous. Anadromus fishes live in seawater but spawn in fresh waters, whereas catadromous fishes live in freshwaters and spawn in the sea. In both cases, fish pass through and use estuarine

resources and thus transform and exchange energy with neighboring ecosystems, constitute a form of energy storage, and function as agents of community regulation. The reasons for such behavior are not known explicitly, but may be due to differences in food resources between adult habitats and spawning grounds, or because spawning grounds represent ''safe sites'' where survival during early life is favored over adult habitats. Because estuaries as we know them today are relatively young on the evolutionary timescale, present migration patterns may reflect prehistoric environmental conditions of which we are only dimly aware.

The use of estuaries by nekton appears to be tuned to seasonal pulsing events that produce periods of greater and lesser productivity and subsequent food availability, and there is coupling between the scales of environmental variability with nekton life history strategies (Yáñez-Arancibia et al., 1988, 1993, 1994; Baltz and Yáñez-Arancibia, 2011). A life history strategy is here defined as a suite of traits such as size at maturity, longevity, fecundity, and parental care, which in combination allow a species to cope with their environment. In contrast, the life cycle is defined as the sequences of stages that a species must go through from the egg to the reproductive adult.

Some estuarine nektons are residents and thus complete their entire life cycle within estuaries. Most nekton species, often referred to as *transient species*, spawn outside of estuaries and use them only for a portion of their life cycle. Transient species are further distinguished between species that must find their way to, and be retained within, the physical confines of an estuary to complete their life cycle (i.e., estuary-dependent species), with those that can survive by associating with estuarylike conditions within an estuarine plume on the inner continental shelf (i.e., estuary-related species; Sánchez-Gil et al., 2008). In all cases, life history strategies have evolved to cope with high variability in winds and littoral currents, salinity gradients, temperature and precipitation regimes, food availability, river outflow, matrices of different habitat types, and aquatic primary productivity that is characteristic of most estuaries, albeit in different and interesting ways.

In recent years, recognition that fisheries, including estuarine fisheries, must be managed in the context of ecosystems has emerged, thus moving beyond the single-species approaches of the past. Improved information about stock boundaries, trophic dynamics, and the magnitude and nature of fisheries landings has required assessment science to adopt approaches that are inclusive of multispecies interactions, and cognizant of the impacts of fishing on habitats and food webs (Pauly, 2010). This represents an enormous challenge to future estuarine and fisheries ecologists because the topics necessary for study are unbounded, ranging in scale from molecular genetics to human ecology. As such, we must look beyond the current tendencies for analyzing and interpreting estuarine nekton community dynamics based on samples of a limited number of mostly valuable species over relatively short time series of observations and interpreting these results in the same limited context. The problems are much bigger now, and we must think bigger to solve them.

In summary, the study on estuarine nekton requires consideration of many concepts over ever expanding temporal and spatial scales, but has few proven theories, and, much more than any other estuarine discipline, requires extensive ecological analysis and interpretations with increasing emphasis on ecosystem-based management and prediction. The relationship of nekton to estuaries is a fascinating story. It is full of subtleties and complexities, which require the study on morphological, physiological, and behavioral adaptations, as well as the integration of nekton life history and estuarine ecosystem ecology (Cowan et al., 2008; Sánchez-Gil, 2009). In this chapter, we present a brief synthesis of what is known about estuarine nekton based on two basic but highly integrated frameworks: (i) estuarine habitats and habitat use, including trophic dynamics, and (ii) life history theory and the strategies that estuarine nekton have evolved to cope with estuarine variability.

13.2 ADAPTATIONS TO NEKTONIC AND ESTUARINE EXISTENCE

13.2.1 Nektonic Adaptations

The principal morphological and physiological adaptations for truly nektonic organisms are the existence and position of body parts used for *swimming* (= *fins and finlets*), a smooth fusiform body, with exception of flatfishes, puffers, pipefishes and a specific gravity reasonably close to that of water. Another important requirement for a nektonic existence is the ability to extract oxygen at a relatively rapid rate from the surrounding water to support the large energy requirements of swimming. And, most pelagic organisms have well-developed sensory organs that are suited to an active, often predatory, nektonic existence. Most fishes have achieved these requirements. For example, many are streamlined and able to control their depth through varying their

specific gravity by changing the amount of gas in the *swim bladder*. Fishes have *gills* well adapted for rapid oxygen exchanges, which permit active and sustained movements. Fishes have developed a sensory system called the *lateral line*, which is very sensitive to sound waves and to changes in water density. Some have also developed *chin barbells*, which help locate food. All these adaptations are well described in the book by Day et al. (1989). Nektonic shrimp and crabs, although less streamlined than fish, tend to be more streamlined than their benthic counterparts.

13.2.2 Estuarine Adaptations

Nekton obviously have general adaptations that allow them to survive in water; however, there are specific adaptations that allow them to flourish in estuaries. One of the most fundamental and intriguing biological questions that can be posed is ''how is it possible for one group of animals to thrive under conditions that would be intolerable for another group?'' (Day et al., 1989). This is particularly interesting when the environment is apparently hostile or stressful. Estuaries are very dynamic and the rapidly changing physical and chemical environment imposes great energy demands on fish, so that most species simply cannot survive there. In fact, the number of species and the number of families found only in estuaries for their entire lives is low, emphasizing that few kinds of fish have evolved to remain in estuaries their entire lives. There are, however, a large number of fish species that spend at least part of their lives in estuaries (Yáñez-Arancibia, 1985). This leads to two intriguing questions that we discuss: (i) If the estuarine environment is so energetically demanding for fish, why have so many groups of fish evolved a life history requiring that some or all of their lives be spent in an estuary? and (ii) Why are these groups so often very abundant?

There are three possible outcomes when an animal encounters stressful conditions, depending on its adaptive capacity: (i) it can migrate to a more favorable environment; (ii) it can adapt, adjust, and survive; and (iii) if conditions are too rigorous, the animal dies. For each species, only a certain portion of the total range of each abiotic environmental factor is compatible with life. Within the relatively large range within which an organism can survive, there is a smaller range where conditions for survival are optimum, that is, where the organisms can have a positive energy balance and can grow and reproduce. Different life stages, especially juveniles, may be adapted to very different environmental conditions compared with adults. Thus, the concept of adaptation is complex and dynamic, especially for estuarine nekton in which young and adults live in very different environments. These differences may allow fishes to avoid competition, optimize growth, or reduce predation.

Before we can answer the question of why so many fish use estuaries for part of their lives, it is necessary to examine specific environmental demands and the organism's response in more detail. Perhaps the most difficult problem faced by estuarine nekton is osmoregulation, which involves maintaining nearly constant internal osmotic conditions in a very changeable external osmotic environment. The relatively impermeable skin, scales, and coat of mucus characteristic of most nekton minimize ion and water exchange associated with changes in salinity. Fish also adjust physiologically by transport of specific ions across the gills, by drinking water, or by controlling the amount of water passed into the urine.

Finally, behavioral mechanisms help fish to avoid extreme situations or conditions. Through active movements, fish avoid large variations outside their physiological tolerances in salinity, temperature, dissolved oxygen (DO), and suspended sediments. For example, many nektonic species move up and down estuaries in response to changes in salinity.

There is paleontological evidence that primitive fishes developed in fresh water and physiological studies confirm that the osmotic concentration of inorganic ions in the blood is less than that in the seawater. This means that all marine fish are preadapted to decreased salinities. Although the skin is relatively impermeable to ions, the gills are by necessity permeable and many marine fish can tolerate reduced salinities if the change is gradual. For estuarine fish subject to tidal changes and sudden floods, the rate of change appears to be as important as the absolute change in salinity.

Many estuarine species breed in the sea presumably because the eggs and embryonic stages are more buoyant in saltwater and intolerant to wide salinity changes, although the turbulence of waves may also be important in keeping the eggs off the bottom. Juveniles, however, rapidly develop a greater tolerance to reduced salinity. Tolerance to the hyper saline conditions that occur in some estuaries during droughts has been recorded in relatively few species. In spite of this wide salinity tolerance by the estuarine fish community from very low salinity to hyper salinity, it has been reported from many parts of the world that the greatest species richness is to be found at the mouth of an estuary (J. H. Day, 1981; J. W. Day et al., 1989) and strongly coupled with pulsing of aquatic primary productivity (Yáñez-Arancibia et al., 1988, 1993). Moreover, there is a distinct range in salinity (3 to 8 practical salinity units) where species

diversity is lowest. Owing to seasonality of tidal range, rainy and dry seasons, floods, winds and evaporation, suspended sediment concentration, and estuarine currents, *osmoregulation* is a major physiological activity of challenge for estuarine nekton, particularly dramatic in tropical and subtropical estuaries.

For temperature, there are different adaptations. It is well known that upper reaches of an estuary are warmer than the sea in summer and cooler in winter. Seasonal changes have marked effects on fish populations, particularly in high latitudes where temperature can become more important than salinity. In cold climates where the whole surface of estuaries may be frozen in winter, the fish population is reduced to a minimum (Day, 1981). Anadromus species that dominate such estuaries have returned to the sea and the overwintering juveniles and resident species remain inactive; they concentrate in the deeper parts of estuaries and show little growth. In temperate estuaries, seasonal changes in temperature are not as marked, but they are equally important. In warm and subtropical estuaries, the significance of temperature declines and salinity effects become more important (Yáñez-Arancibia, 1985). In such estuaries, the rainy season may be a critical ecological period in the year, and the immigration of juveniles can be conditioned by frontal winds, river discharge, and pulses in primary productivity. In tropical estuaries, there often are smaller seasonal changes in temperature, but there are marked changes in salinity.

Temperature and salinity may operate synergistically. Reduced or fluctuating salinity in combination with varying temperature offers special physiological problems for osmoregulation for most species. For example, plaice (a flatfish) is euryhaline at low temperature and eurythermal at high salinities. However, they do not thrive in low salinity, warm location conditions because they cannot survive the combination of physiological stressor (Day et al., 1989). For the temperate zone, it may be considered a general rule that an increase in water temperature leads to reduced ability to withstand wide variations in salinity, possibly because of the effect of warm temperatures on enzymes that regulate osmoregulation in estuarine nekton.

13.2.3 Feeding Adaptations and Nektonic Food Web

Fishes have evolved a number of characteristic adaptations for feeding. Even though many estuarine fish have diverse diets, most possess adaptations that increase the probability of successfully handling and ingesting a particular group of prey. Differences in the size and position of mouth, kind and position of teeth and branchial arches, and shape and length of intestines all have important consequences for food capture and use. More details about the nature of feeding adaptations can be found in ichthyology text books. Suffice it to say that estuarine fishes taken as a whole are capable of feeding at every trophic level in the food web, and in any estuarine habitat. Catfishes (Ariidae), for example, usually have distinctive whiskerlike barbells, smooth scale-less bodies, and sharp barbed spines at the margins of their pectoral fins. All catfishes move along the bottom searching for food with ''taste buds'' located on their barbells. The barbells play an important role in searching for food since visibility is generally poor in turbid estuarine waters. Catfish are omnivorous bottom feeders often ingesting many different types of prey (Yáñez-Arancibia and Lara-Dominguez, 1988).

Flatfishes are immediately recognizable by their laterally-compressed bodies and their asymmetrical eyes, both of which are on the dark-colored top sides of their bodies. Most flatfishes begin life with normally arranged eyes. With growth, metamorphosis occurs and the eye of the side that is on the bottom migrates to the other side and a rearrangement of internal organs also occurs. Most species prefer soft muddy or sandy bottoms where they lie buried in sediment when at rest. The hogchoker (*Trinectes* sp.), baywhiff (*Citharichthys* sp.), and blackcheek tonguefish (*Symphurus* sp.) are small flounders with wide distribution. The summer (*Paralichthys* sp.) and winter (*Pseudopleuronectes* sp.) flounders are large, with a more northern distribution, and are prized by sport and commercial fishermen. The smaller flounders eat small crustaceans, worms, and mollusks; the larger flounders also consume larger shrimps, crabs, and fish (Sánchez-Gil, 2009), particularly *Scyacium gunteri*, *Citharichthys spilopterus*, and *Etropus crossotus* in the southern Gulf of Mexico. It is important to note that flatfishes, as well as many other estuarine transient species, can find suitable habitat beneath estuarine plumes on the shallow shelf in many linked estuarine-river plume ecosystems.

Because a large mouth intuitively seems to be a good way to increase the probability of prey capture, we may wonder why not all fish have huge mouths. One answer is that selective pressures acting to favor particular shapes or positions of the mouth often conflict. In some cases, one selective pressure has been more important than another, resulting in a mouth design that has important implications for food acquisition. To eat a wide range of prey sizes, a mouth should be large to feed on small prey. Fish compromise by changing the location of the mouth

and the size in accordance with how they can eat. Common first-order consumers in estuaries, such as mojarras (*Gerres* sp., *Eucinostomus* sp., and *Eugerres* sp.), often have extremely conspicuous modifications of the jaw bones so that the mouth can protrud to enable feeding on small prey and on the leaf surfaces of plants such as sea grasses (Aguirre-Leon and Yáñez-Arancibia, 1986).

Fish with a superior (located more dorsally) mouth, such as silversides, often suck in floating insects from the water surface. Second-order consumers, such as *Orthopristis crysoptera*, Pomadasyidae, that feed on small benthic organisms and on leaf surfaces of *Thalassia* leaf have an intermediate, sized inferior mouth (located below the tip of the snout) mouth. Top predators such as trout, which usually pursue other fish species, have a large, terminal mouth, while demersal fish such as hake (*Urophyscis* sp.) also have inferior mouths. The bottom-oriented seacatfishes (Ariidae) have a large terminal-ventral mouth and distinctive barbells for food searching. Some fish, such as croakers, which use both the pelagic and benthic pathways equally, have compromised and inferior mouths.

Although food is collected by mouth, the real processing takes place in the throat or pharynx, where the pharyngeal bones are located. Often a wide range of dental development is associated in a predictable way with the types of food eaten. The number, size, and structure of teeth on these bones differ according to food type most commonly processed. At the most fundamental level, it is generally true that active predators have strong jaws with sharp teeth. The surfaces of the pharyngeal plate of phytoplankton eaters, such as shad, are covered with rows of fine recurved teeth so that when the two sets slide together, the algae are combed backward. Fish eaters, such as trout, tend to have sharply pointed teeth that point backward. These teeth grip and force backward fish held in the mouth. Mollusks eaters, such as black drum, posses massive pharyngeal teeth with a number of large flat ''molars'', which crack the shells of the prey and a similar modification occurs in the Tetraodontidae (e.g., *Sphoeroides testudineus*) in tropical estuaries.

Modifications of the branchial arches and gill rackers, which aid in food selection and processing, have received much attention. The presence of numerous, long, thin, and closely spaced gill rackers on the inward side of the gill arch indicates a fish species that filters plankton from the water. The appearance in a single fish species of elaborate gill-racker modifications during development and accompanying dietary shifts has been demonstrated. For example,

the change from a zooplankton diet to a phytoplankton diet in Atlantic menhaden (*Brevortia thyrannus*) is accompanied by an increase in the number, length, and complexity of gill rackers. Similarly, the initiation of phytoplankton feeding by the anchovy (*Engraulis anchoveta*) is correlated with the formation of elaborate gill rackers. Predatory fishes often have tooth-shaped gill rakers that facilitate the capture and retention of large prey items.

Once the food has been captured and consumed, the ability of the fish to use the food is dependent on the digestive process. In general, the length and complexity of the gut increases from top carnivore to herbivore, being extremely long in detritus consumers such as *Mugil curema*. This is a response to the digestibility of the food item. Top carnivores generally consume fish or invertebrates, which are primarily protein and are easily digested and assimilated. Plant tissue or detritus are structurally complex foods composed of difficult to digest carbohydrates, lignin, and cellulose. For this reason, herbivores have long, frequently blackened, guts, which increase the time the food spends in the intestine and provides a longer time period for enzymes to break down the more complex organic compounds. Blacked guts in herbivores prevent photosynthesis from occurring in the gut while the plants are being digested. Many species have a gut flora of cellulolytic bacteria that participate in the enzymatic hydrolysis of food. Many herbivores also have highly acidic guts, which cause a chemical breakdown, and gizzard that grinds the food into small particles before it enters the intestine.

The most diverse of the demersal nekton are croakers, cods, mullets, stingrays and skates, as well as shrimps, crabs and small squid. Within these fishes, there are two feeding types. The first are *bottom feeders*, similar to catfish, with inferior mouths and often barbells on the lower jaw. These species eat mostly benthic invertebrates, including small crustaceans, annelids worms, and small mollusks (Sánchez-Gil, 2009). Three members of this group widely distributed along the Atlantic coast of North America are the Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and silver perch (*Bairdiella* sp.). Cods (*Gadus* sp.) and hake (*Urophyscis* sp.) are common members of this group in northern estuaries in North America and Europe, while mullet (*Mugil* sp.) are more typical in temperate, tropical and subtropical estuaries. These fish usually congregate in loose monospecific schools and forage along the bottom or on aquatic plants such as (*Ulva* sp.). Some species change their bottom preference from muddy to firmer substrates, as they grow older. The second feeding type is the *mobile predator*, top carnivores,

which are only loosely associated with the bottom, feeding on more motile prey such as peneid shrimps and pelagic fishes. Typically, estuarine top carnivores include the sea trouts, (*Cynoscion* sp.), sea basses (*Morone* sp.), bluefish (*Pomatomas saltitrix*), jacks and small coastal sharks.

Because nekton, including estuarine nekton, have developed a wide range of feeding adaptations, most any have a broad trophic spectrum, often feeing on 10–20 or more different trophic groups. These broad feeding options aid in recruitment and ensure their survival during the critical stages of ontogeny (Yáñez-Arancibia, 1985). Because of these factors, trophic spectra change with locality or habitat in the ecosystem (different food availability), the size of the fish (different food needs), the season of the year (changes in food types available), and the time of the day/night cycle (live food behavior).

For example, it is not unusual for estuarine nekton to show a great affinity for particular habitats, often concerning a particular stage of their life cycle. Secondary consumers (fish that feed on primary consumers) are often demersal fish and are not limited to a certain habitat but usually have a wide distribution inside the estuarine ecosystem. Secondary consumers are the most important in determining particular characteristics of tropical/subtropical estuarine fish communities, due to their high diversity, numerical abundance, and wide trophic spectra and habitat specificity during the distinct stages of their life cycles. In the Pacific coast of Mexico tropical estuaries, with more than 100 fish species, secondary consumers represent more than 50% of the total species number. At the same time in the southern Gulf of Mexico, in communities with more than 140 fish species, more than 50% are secondary consumers (Yáñez-Arancibia, 1978, 1985; Yáñez-Arancibia and Sánchez-Gil, 1986). Estuarine fish feed, in the course of their ontogeny, on a succession of different food types, often gathered from different subareas within a given estuary. Thus, the whole trophic structure, in dynamic terms, does not consist of specific trophic levels, but rather, it is a complex of multidimensional biological interactions and variability in space and time. The complexity of diets in estuarine nekton reflect changes in food preferences and sources as fish grow (ontogenetic changes) and the opportunistic nature of most fish species. The considerable variations in types and amounts of foods consumed by a species at a given location, and the similarity of major food types eaten by different species at a given location, demonstrate that diet composition of omnivores is often determined mostly by food availability. Future research in trophodynamic ecology in estuarine fish communities should be oriented in this direction.

Fishes differ greatly in the character of the food they consume. However, many show a basic dependence on phytoplankton and organic detritus (e.g., from sources such as salt marshes, sea grass, and mangroves) through both pelagic and benthic pathways. The pelagic pathway begins with phytoplankton and goes to copepods, decapods, and mysids or other mesozooplankton to small fishes such as anchovy and herring and then to top carnivores. The benthic pathway begins with detritus and other organic matter, which is consumed by benthic copepods and polychetes as well as filter-feeding organisms and then small benthic dwelling fish, which in turn also are eaten by large predators such as Sciaenids, Lutjanids, and others carvivorous fishes.

In summary, the feeding relationships among estuarine fishes suggest at least seven ecological generalizations for the estuarine food webs: (i) nekton comprise most of the midlevel and top carnivores (i.e., second- and third-order consumers); (ii) diets change with ontogenetic development, growth, food availability, and locality within an estuary; (iii) there is flexibility of feeding in time, space, and environmental pressure; (iv) the most abundant food resources are shared among many species, in a seasonally programmed use that avoids intense interspecies competition; (v) estuarine nekton often use both pelagic and benthic pathways taking food items from different levels of the food web; (vi) in the food web, the most diverse and abundant fish are omnivorous and opportunistic second-order consumers of all sizes; and (vii) the overall trophic structure, in dynamic terms, does not consist of specific trophic levels, but rather it is a complex of multidimensional web (i.e., food web) of biological interactions in space and time in which fish couple both pelagic and benthic pathways of energy flow.

13.3 THE ESTUARINE ECOSYSTEM AS HABITAT FOR NEKTON

As habitat, estuaries offer both opportunities and present challenges to nekton. We have already learned that land-margin ecosystems are dynamic environments, often with steep gradients in temperature and salinity that change rapidly in response to tides, seasonal changes in freshwater inflow, and weather. Estuaries occur worldwide in climates ranging from boreal to tropical, from arid to humid,

and in basins from small lagoons to very large drowned river valleys such as Chesapeake Bay. In addition, many occur in built environments in the form of deltas at the mouths of large rivers such as the Mississippi, Nile, and Yangtze. As such it is difficult to generalize about how nekton use estuaries and the habitats they contain. That said, because of the conditions described above, estuarine diversity and food webs tend to be relatively low and simple, respectively, especially among the estuarine residents, because relatively few nekton can deal with the high variability typical of estuarine environments. This does not mean, however, that estuaries are not used extensively by nekton. In fact, nekton abundance and biomass in estuaries can be among the highest in the world, and species that use estuaries for all, or a portion, of their life cycle, can experience very high growth rates (>30% increase in weight each day), hence secondary productivity; this is especially true for species that use estuaries as nursery areas for some portion of their early life (Pauly and Yáñez-Arancibia, 1994; Yáñez-Arancibia et al., 1994; Able, 2005; Cowan et al., 2008).

As a means by which to organize vast amounts of information, we summarize the results of extensive reviews of European (Elliott and Hemingway, 2002), North American (Able and Fahay, 1998; Nordlie, 2003), and Tropical (Yáñez-Arancibia, 1985; Yáñez-Arancibia et al., 1988, 1993, 1994) estuaries to arrange the following sections on habitats and habitat use, and draw heavily from Roff (1992) and Polis and Winemiller (1996) in our discussion of life history theory and strategies. We combine the information to describe the types of fishes that are characteristic of estuarine environments.

13.3.1 Estuarine Habitats

To begin, we focus on the two factors regarding nursery function and the high abundances of juvenile nekton in estuarine environments by addressing the questions: (i) Are they attracted as predators to high prey densities in these areas? (ii) Or do the habitats provide juveniles with protection from predation? We say loosely because difficulty arises almost immediately when facing these questions because estuaries consist of a complex mix of many distinctive habitat types and these habitats do not exist in isolation. Rather, there are physical, chemical, and biological links between them. For example, they can be linked via sediment transport, transfer of nutrients, and in the way mobile animals move between them ontogenetically, seasonally, and during a single tidal cycle (Yáñez-Arancibia and Day, 1982). The relative value of any habitat ''patch'' may depend on its proximity

and/or degree of connectivity to other habitats and when during the life cycle a habitat is used by a nekton species. While understanding processes determining nursery function is necessary to develop restoration and preservation programs, and for development of ecosystem-based management approaches, we lack complete understanding of how prey/predator interactions act to determine the value of an estuarine nursery. Even among estuary-dependent nekton, we know that both increased feeding opportunities and decreased vulnerability to predation together increase the survival potential of young nekton while they are in an estuary.

Ignoring the connectivity issue for a moment, distinct habitat types do exist, and the following encompass all major categories/zone found in estuaries. These habitats are (i) tidal fresh water; (ii) reed beds and other emergent vegetation in fresh, intermediate, and brackish marshes; (iii) salt marsh and mangroves (intertidal vegetated habitats); (iv) intertidal soft substratum; (v) intertidal hard substratum; (vi) subtidal soft substratum; (vii) subtidal hard substratum; (viii) subtidal sea grass beds (subtidal vegetated habitats); and (ix) biogenic reefs. The pelagic part of water column above, or those areas that are inundated by water, are considered part of each of the above habitats.

Before we discuss habitat use, a brief description of each habitat type is in order. These descriptions are largely taken from Elliot and Hemingway, (2002).

1. *Tidal fresh waters* are those waters upstream of significant salt water influence, with salinities usually less that 0.5 ppt, and where water movement is highly dynamic and tidal, including tidal reversals in the direction of river flow. The extent of this zone depends on the ratio of fresh water to tidal volume, thus climatology, tidal range, and morphology of the basin. Channels in the tidal fresh water region of an estuary are typically more steep-sided and narrower than downstream in the estuary, so there is a narrow intertidal zone. Subtidal and intertidal habitats in this region are usually composed of mobile substrates, from fine silts to sand and coarse gravel. Subhabitats include intertidal soft substrate (sediment banks and shoals), subtidal soft substrate, creeks, bayous, and backwaters. Reed beds and other emergent vegetation may form a significant subhabitat in the tidal fresh portion of an estuary.

2. *Reed beds* are dense stands of herbaceous plants that occur in low salinity zones, upstream of the turbidity maximum, usually in waters ranging from 0 to 5 ppt. The dominant flora in reed

beds are members of the genera *Phragmites* and *Phalaris*, which form dense beds in upper intertidal zones, but may form shallow, permanently subtidal areas in nontidal estuaries. The spatial extent of reed beds in an estuary is linked to length of tidal freshwater zones. If the beds stay continuously flooded, they always are accessible to fish, but they are less accessible if the beds occur in intertidal areas. Subhabitats within reed beds include open water areas, creeks, and bayous.

3. *Salt marsh and mangroves* are intertidal, sediment-based, macrophyte-dominated, saline-influenced habitats that occur from mean high water to the upper shore where, in undisturbed systems, habitats inland (e.g., higher elevations) of salt marshes and mangroves may undergo a transition to brackish, freshwater, or terrestrial habitats. Typical mangrove (''amphibian trees'') species are *Rhizophora, Avicennia, Connocarpus*, and *Laguncularia*. Salt marsh develops where waters are sufficiently quiet to allow sediments to settle, and where conditions are suitable for settlement and growth of a limited number of halophytic plant species. Salt marsh and mangroves both separately and together form complex mosaics in estuaries with other intertidal subhabitats such as mudflats. Development of linear or dendritic creeks is a feature of mature marshes; these creeks are points of entry to marsh environments for nekton. Surface pools or ponds exhibit low nekton diversity because of the harsh conditions in the ponds. Other subhabitats in salt marshes include mud flats and mud walls.

4. *Intertidal soft substrates* are unvegetated intertidal habitats that are composed of sediments ranging from fine silts to coarse sands. These areas are largely free of higher plants, but usually are coated with blue-green algae and diatoms, and frequently contain high densities and high biomass of macrobenthos. As such, these areas provide food for estuarine nekton during high tides. Subhabitats include creeks and banks, pools of standing water, intertidal patches of sea grasses, and extensive beds of bivalves such as oysters and mussels and dense beds of ephemeral macroalgae such as *Ulva* sp.

5. *Intertidal hard substrates* are vegetated or unvegetated intertidal habitats lying between the highest and lowest tide lines and are composed predominantly of hard substrate ranging from gravels to bedrock in temperate and boreal climates to ancient coral outcroppings in the tropics. These habitats usually are referred to as *rocky intertidal zones* and have been the sites of many important studies concerning competition for space in marine and estuarine ecosystems. These habitats usually exhibit dramatic zonation with elevation. Macroscopic algae such as kelps are often dominant near and just below the low tide line, mussels and other bivalves a little higher up, and barnacles and limpets in areas closest to the high tide line. Subhabitats include tide pools that frequently exhibit much higher biodiversity than the rock substrates themselves.

6. *Subtidal soft substrates* are permanently subtidal unvegetated habitats, composed predominantly of sediments ranging from silts to coarse sands, generally lying below the level of lowest tides. In tidal estuaries, these areas typically support lower densities and biomass of benthic invertebrates than adjacent intertidal areas of soft substrate. It is generally recognized that low densities and biomass of benthos in these areas are mostly attributable to high consumption rates by juvenile nekton. Subtidal soft substrates are found in creeks and bayous, main channel areas, deeper water areas, backwaters, and lagoons. Subhabitats include patches of sea grasses, extensive beds of bivalves such as oysters and mussels, and dense beds of ephemeral macroalgae such as *Ulva* sp. if the overlying water is shallow enough.

7. *Subtidal hard substrates* are vegetated or unvegetated habitats below the level of the lowest tides and are composed predominantly of hard substrate ranging from gravels to bedrock. These habitats are found mostly in estuaries that present colder climates and in fjords. Simply put, they are the subaqueous reaches of the rocky intertidal zones described above. As such, they often are dominated by large plants such as kelps and other fucoids, and by bivalves such as oysters and mussels, but can be almost devoid of vegetation in areas where wave energy is very high.

8. *Subtidal sea grass beds* are vegetated habitats in soft substrata that are dominated by halophytic macrophytes adapted to complete and continuous submergence in water of low to high salinity. Sea grasses may form extensive beds that are relatively stable over time, adding considerable vertical structure (up to 1 m in height) to the soft substratum environments on which they develop. Important genera of estuarine sea grasses include *Zostera, Thallassia, Halodule*, and *Ruppia*. In some lagoons and other brackish water habitats, beds of stonewarts or charophytes (complex algae that often are encrusted with $CaCO_3$) can be important

structural elements as well. Subhabitats within sea grass beds include newly developed or regenerating patches of sea grass following seasonal dieback or disturbance, as these have a very different topographical profile relative to mature beds. Other subhabitats include patches of bare substrate surrounded by sea grass and biogenic reefs surrounded by sea grass.

9. *Biogenic reefs* form elevated structures or extensive epibenthic beds, can be either intertidal or subtidal, and are built by calcareous or other concretion-forming organisms or by surface-dwelling bivalves (e.g., oysters). Extensive beds of bivalve mollusks (e.g., *Mytilus, Ostrea, Crassostrea*, and *Modiolus* sp.) add considerable heterogeneity to substrates on which they develop. Biogenic reefs can also be built by corals or by sabellid or serpulid polychaete worms. Mature biogenic reefs can have high vertical relief with much complexity. Subhabitats may include pools of standing water during low tide and many interstitial spaces for cryptic estuarine nekton.

In most estuarine systems, these habitats combined account for practically all of the total area. The diversity and areal extent of habitats worldwide is hard to generalize but tends to scale roughly with tidal range and temperature. The most extensive and widely distributed habitat is subtidal soft substrate, which is found in boreal, temperate, and tropical regions and accounts for about 50% of total estuarine area worldwide. Intertidal soft substrate is the second most extensive, accounting for almost 30% of total estuarine area, but is far more prevalent in areas with high tidal ranges. Wetlands (salt marsh and mangroves) are third most extensive, accounting for more than 10% of estuarine area worldwide, but may be more extensive in microtidal areas such as the Gulf of Mexico coast. Subtidal sea grass also accounts for more than 10% of estuarine habitat worldwide, but sea grass beds or meadows are most extensive in the tropics. The remaining five habitats (subtidal hard substrata, tidal freshwater, reed beds, intertidal hard substrata, and biogenic reefs) generally contribute less than 5% of the total surface area in all regions but can be locally important depending on estuary location and conditions.

13.3.2 Habitat Use by Estuarine Nekton

To evaluate habitat use, let us consider four different functions that estuarine habitats can facilitate: (i) spawning, (ii) nursery, (iii) feeding, and (iv) migration. Spawning grounds are areas where mating occurs or eggs are deposited or released. Estuary spawners include residents or others species that use estuaries only to spawn because circulation patterns permit local retention of eggs and larvae. Nursery grounds are areas where juveniles aggregate via active or passive transport mechanisms but usually are spatially or temporally separated from adults. Survival of juveniles is enhanced through better feeding conditions, optimal growth, and/or refuge opportunities, and thus may be considered ''safe sites'' from which recruitment to adult populations follows (and may be dependent on) nursery usage. Feeding grounds are used by nekton making feeding migrations into habitats where they preferably or exclusively forage, often as adults. Many of these species are transient and migrations may be tidal, diurnal, or seasonal. Diadromy obligates nekton to migrate between marine and fresh waters for spawning, and in many cases, an estuary is the only path fish can follow. In doing so, migrating nekton use some habitats but not others. One further use of estuarine habitats may be refugia, but this is less straightforward. It is difficult to define ''refuge'' as a habitat usage, even though use as a refuge from predation seems like a simple concept. This issue is difficult because refuge value is hard to isolate if nekton also use a habitat for other reasons such as feeding.

13.3.3 Species Richness and Distribution Between Habitats

The following statements are based on data summarized from a variety of estuaries around the world. The number of fish species reported from estuaries ranges from as few as 24 in the Ebro estuary in Spain to more than 150 in Terminos Lagoon on the Gulf of Mexico to more than 400 in the extremely rich lower Amazon River in Brazil. The mean number in Europe and North America is 57 species. Accordingly, as seen in Table 13.1, there is no apparent trend with latitude, but this may be attributable to the intensity of study in different areas. Table 13.1 must be viewed with caution because we are not considering tropical America and South East Asia estuaries. The distribution of species richness over the nine habitats described above is shown in Figure 13.1, separated by latitude low (tropics), mid (temperate), and boreal (high).

It is clear that most species are found on subtidal soft substratum (habitat 6), subtidal hard substrate (habitat 7), subtidal sea grass beds (habitat 8), and biogenic reefs (habitat 9). Fewer species occur in salt-marshes (3) and reedbeds (2). These latter habitats are not always flooded, so they are harsher environments

TABLE 13.1 The HUI calculated for European estuaries

Habitat/Number	HUI[a]
Tidal freshwater	23.1
Reed beds (2)	15.5
Saltmarsh (3)	19.3
Intertidal soft substrate (4)	37.6
Intertidal hard substrate (5)	9.0
Subtidal soft substrate (6)	69.7
Subtidal hard substrate (7)	43.3
Subtidal sea grass beds (8)	46.5
Biogenic reefs (9)	20.7

Abbreviation: HUI, habitat utilization index.
[a]HUI index represents the sum of fish life history stages using a single habitat divided by the number of sites for that habitat in all estuaries combined (Elliot and Hemingway, 2002).

FIGURE 13.1 The distribution of fish species richness in estuaries by habitat type and latitude. *Source:* From Houde (1989).

for nekton. The contribution of commercial species is generally more than 50% in southern estuaries and is less than 50% in the north. In the Gulf of Mexico, perhaps as many as 65–75% of commercially important species are estuary related or estuary dependent (Gunter 1963; 1967; Longhurst and Pauly, 1987; Sánchez-Gil and Yáñez-Arancibia, 1997).

While it is common for species to use multiple habitats, there are different peaks of abundance regulated by climatic changes that control the biological and physical characteristics of the habitats (Fig. 13.2a,b). In the tropics, the use of habitats at different times is the result of different population structure and dynamics. The wide spatial distribution of these species in multiple habitats allows for niche partitioning among species and different life stages of the same species (i.e., different biological stages occur in different habitats). From Figure 13.2, we see that there is preferential use of a fluvial lagoon system (Fig. 13.2a) during the wet season, while the sea grass mangrove system is preferred (Fig. 13.2b) habitat during the dry season.

13.3.4 Habitat-Specific Use: Functional Relationships

By habitat, the results for use are similar to those for species richness (Fig. 13.3). Most species use subtidal soft substrate (6), subtidal hard substrate (7), subtidal sea grass beds (8), and biogenic reefs (9) for feeding and nursery areas, with intertidal soft substrate also being important for feeding. Fewer estuarine fishes use saltmarsh (3), reed beds (2), and tidal fresh (1) areas for these same functions. At the species level, compiled from data from all well-studied estuaries, the percentage of the total number of fish species

undertaking different habitat uses (functional relationships) are in rank order as follows: feeding: 76% > nursery: 63% > spawning: 24% > diadromy: 9%. These percentages do not sum to 100% because some species use estuaries for more than one function. Comparatively speaking, there are only a few diadromous species, and most transient species do not spawn in estuaries. It is important to note that the feeding versus nursery results are reversed in more southern estuaries where nursery function apparently is more important. Other than that, there does not appear to be a strong relationship between latitude and how estuaries are used by nekton.

In their comprehensive review of European estuaries, Elliot and Hemingway (2002) combine form (habitat type) and function (usage) in a useful semi-quantitative index of habitat use that includes habitat use by life history stage (eggs, larvae, juveniles, and adults). This takes into account whether the fishes are estuary residents or transients and includes diadromous species that often migrate through an estuary to spawn as adults, while both adults and early life history stages can migrate out. The habitat utilization index (HUI) is the sum of life history stages using a single habitat divided by the number of sites for that habitat in all estuaries combined. This index approximates the overlap between fish life history stages and the overall usage of each habitat type, and their results are shown in Table 13.1.

The HUI evaluates a habitat on the basis of an average number of uses made by all species and all life stages, but the rankings, however, come out almost the same as before (Fig. 13.1): subtidal soft > subtidal sea grass > subtidal hard > intertidal soft > tidal fresh > biogenic reefs > saltmarsh > reed beds
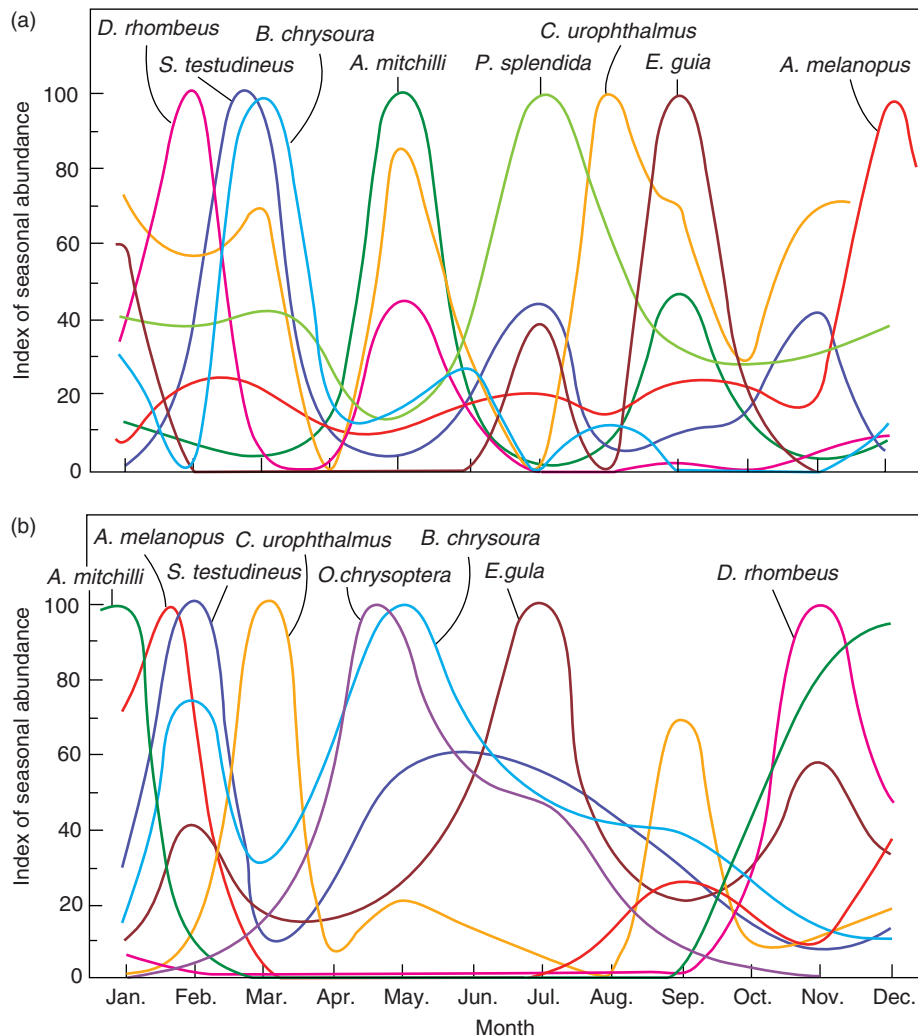
FIGURE 13.2 Seasonality of abundance for nine dominant fish species in tropical Terminos Lagoon southern Gulf of Mexico. The index of abundance both in (a) fluvial lagoon system (FLS) and (b) sea grass mangrove system (SMS) habitats, shows a clear seasonal programming of fish species and sequential habitat utilization. *Anchoa mitchilli, Arius melanopus, Sphaeroides testudineus, Cichlasoma urophthalmus, Bairdiella crysoura, Eucinostomus gula*, and *Diapterus rhombeus. Orthopristis chrysoptera* is exclusive from SMS, and *Petenia splendida* is exclusive from FLS. *Source:* From Yáñez-Arancibia et al. (1988).

> intertidal hard. It should be apparent by now that habitat complexity is only one part of the equation that determines the relative value of a particular habitat type to estuarine nekton. The HUI also does not sum to 100%, stressing the fact that estuaries should be viewed as a matrix of interconnected habitats that can be used by many species for the same or different functions, and for any single species, it can be used for different functions depending on their life history stage.

In summary, the habitat attribute that is most important to facilitate use by estuarine nekton is the frequency of inundation, that is, how often the habitat is covered by water. Habitats that are always flooded

are the habitats that are most well utilized by estuarine fishes and other nekton species (Fig. 13.2a,b). Among the habitats that are always flooded, subtidal soft substrate is the largest by areal extent and also provides excellent feeding and nursery grounds for estuarine nekton. The structural complexity of subtidal sea grasses and subtidal hard substrate is also important for feeding and refuge, showing that habitat complexity is an important attribute as well. Use by nekton in terms of habitat type and function does not vary significantly with latitude, suggesting that strong local gradients in factors such as temperature and salinity, or high variability among a variety of factors, create conditions to which relatively few

species, especially residents, can easily adapt. Those that have adapted are constrained to relatively few uses by the aforementioned estuarine1 characteristics.

13.4 LIFE HISTORY STRATEGIES AMONG ESTUARINE NEKTON: NOTES ON IMPORTANT REPRESENTATIVE TAXA

13.4.1 Life Cycles and Life Histories

Given that conditions for nekton in estuaries are highly variable, it is not surprising that relatively few fish families have members that have adapted to these conditions and that estuaries worldwide share many of the same taxa (Table 13.2). In fact, from the study by Potter et al. (1990), eight families have members that are common to estuaries in Western Australia, South Africa, North America, and Western European (i.e., four continents). Nevertheless, if we consider Table 10.1 in the study by Day et al. (1989) on page 380 from Estuarine Ecology, First Edition, we integrate in Table 13.3 the most typical examples of estuarine nekton communities, presenting some selected families, genera, and species around the world.

From a life history standpoint, estuarine fishes exhibit a wide variety of strategies, but they can be largely grouped into three categories: (i) freshwater spawners, (ii) estuarine spawners, and (iii) marine spawners (Deegan and Thompson, 1985; Pauly and Yáñez-Arancibia, 1994; Yáñez-Arancibia et al., 1993, 1994). Within each of these categories, life history strategy can be further defined based on traits that together make it possible for estuarine nekton to persist in estuarine conditions that vary at many temporal and spatial scales. In a series of studies in Terminos

TABLE 13.2 Solubilities of nitrogen, oxygen, argon, neon, and helium in seawater at a salinity of 35

Family	Western Australia	South Africa	North America	Western Europe
Clupeidae	X	X	X	X
Atherinidae	X	X	X	X
Terapontidae	X	—	—	—
Mugilidae	X	X	X	X
Gobiidae	X	X	X	X
Engraulidae	X	X	X	X
Tetraodontidae	X	y	X	X
Apogonidae	X	—	—	—
Sillaginidae	X	—	—	—
Gerreidae	X	—	X	—
Plotosidae	X	—	—	—
Sparidae	X	X	X	X
Arripidae	X	—	—	—
Hemirhampidae (Exocoetidae)	X	X	X	X
Pomatomidae	X	X	X	X
Carangidae	—	X	X	X
Platycephalidae—	X	X	—	—
Monodactylidae	—	X	—	—
Soleidae	—	X	—	X
Haemulidae	—	X	—	—
Ambassidae	—	X	—	—
Sciaenidae	—	X	X	X
Ariidae	—	X	X	—
Clinidae	—	X	—	—
Syngnathidae	—	X	X	X
Cichlidae	—	X	(X)	—
Blenniidae	X	X	X	X
Galaxiidae	—	X	—	—

(X) for Cichlidae indicates several nonindigenous species.
[a] *Source:* From Potter et al. (1990).

TABLE 13.3 Typical examples of estuarine nekton communities: fish families[a]

Shallow Water Fishes		Tropical	Temperate		Boreal
			Subtropical	Cold	
Killifish Cyprinodontidae *Cyprinodon*		▮	▮	▮	
Silversides Atherinidae *Menidia*		▮	▮	▮	
Cardinalfish Apogonidae *Apogon*		▮	▮		
Asiatic glassfishes Ambassidae *Ambassis*		▮	▮		
Molly Poeciliidae *Poeciliopsis*		▮	▮		
Cichlids, Tilapia Cichlidae *Cichlasoma* *Oreochromis*		▮	▮		
Tigerperches Terapontidae *Amniataba*				▮	▮
Stickleblacks Gasterosteidae *Apeltes*				▮	▮
Herring Clupeidae *Brevortia* *Sardinella*		▮	▮	▮	
Halfbeaks Hemiramphidae *Hemiramphus*		▮	▮	▮	

(*Continued*)

TABLE 13.3 (*Continued*)
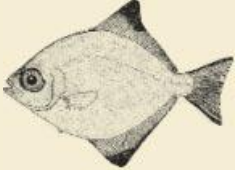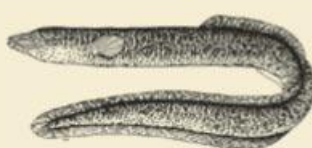
Shallow Water Fishes		Tropical	Temperate		Boreal
			Subtropical	Cold	
Moonyfishes Monodactylidae *Monodactylus*		▇	▇		
Anchovies Engraulidae *Anchoa* *Engraulis*		▇	▇		
Australian salmon Arripidae *Arripis*		▇	▇		
Bluefish Pomatomidae *Pomatomus*		▇	▇		
Jacks, drums Carangidae *Chloroscombrus*		▇	▇		
Salmon Salmonidae *Coregonus* *Oncorhynchus*				▇	▇
Freshwater eels Anguillidae *Anguilla*		▇	▇		
Mullets Mugilidae *Mugil*		▇	▇		
Soles Soleidae *Trinectes*		▇	▇		
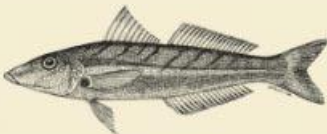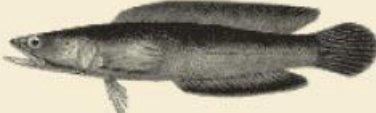
TABLE 13.3 (*Continued*)
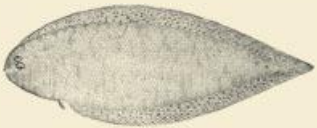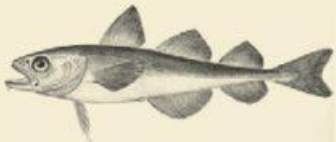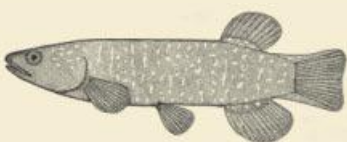
Shallow Water Fishes		Tropical	Temperate		Boreal
			Subtropical	Cold	
L-Flounders Bothidae *Citharichthys* *Paralichthys*		██████████████████			
Drums, croakers Sciaenidae *Bairdiella* *Micropogonias* *Cynoscion*		██████████████████			
Pipefish, seahorses Syngnathidae *Hemiramphus* *Hippocampus*		██████████			
Gobies Gobiidae *Gobionellus*		██████████			
Combtooth blennies Blenniidae *Ecsenius*		██████████			
Silver jenny Gerreidae *Eucinostomus* *Eugerres*		██████████			
Catfish Ariidae *Arius*		██████████			
Porgies Sparidae *Archosargus*		██████████			
Puffers Tetraodontidae *Sphoeroides*		██████████			
Grunts Haemulidae *Orthopristis*		██████████			

(*Continued*)

TABLE 13.3 (*Continued*)

Shallow Water Fishes	Tropical	Temperate		Boreal
		Subtropical	Cold	
Smelt-whitings Sillaginidae *Sillagus*	███	███		
Eeltail catfishes Plotosidae *Neosilurus*	███	███		
Flatheads Platycephalidae *Platycephalus*	███	███		
Ponyfishes Leiognathidae *Leiognathus*	███	███		
Seabasses Serranidae *Diplectrum*	███	███		
Snappers Lutjanidae *Lutjanus*	███	███		
Threadfin Polynemidae *Polydactylus*	███	███		
Milkfish, snakehead Channidae *Channus*	███	███		
Phycid hakes Phycidae *Urophycis*	███	███		
R-Flounders Pleuronectidae *Pseudopleuronectes*		███	███	

TABLE 13.3 (*Continued*)

| Shallow Water Fishes | Tropical | Temperate | | Boreal |
		Subtropical	Cold	
Tonguefish Cynoglossidae *Symphurus*		███████████	██████	
Temperate basses Perchtyidae *Morone*		███████████	██████	
Striped bass Moronidae *Morone*		███████████	██████	
Codfish Gadidae *Gadus* *Microgadus*			██████	██████
Smelts Osmeridae *Osmerus*			██████	██████
Sculps Cottidae *Artediellus*			██████	██████
Galaxiids Galaxiidae *Galaxias*			██████	██████

[a]Sources of information: FishBase, http://www.fishbase.org, and FAO, http://www.fao.org. Figures represent the families' general shapes, and genus are typical examples. Shadow area means distribution. From a didactical point of view, fish families have been arranged following the typical habitats described in the text.

Lagoon southern Gulf of Mexico (Fig. 13.4), the use of mangroves habitat was clearly illustrated. There are clear connections among seasonal pulsing of mangrove detrital production, adjacent planktonic and sea grass productivity, and fish movement and secondary productivity. It is reasonable to extrapolate from this and similar studies that the removal of mangrove wetlands would cause a significant decline in sport and commercial fisheries in adjacent open waters.

To better account for the many different ways nekton have evolved to cope with their environments, Winemiller (1989) developed an ordination of life history characteristics in a trilateral continuum that reflects an adaptive surface area based on fecundity, age of maturity, and juvenile survivorship (Fig. 13.5).

In some ways, this approach is similar to that which denotes R versus K-selected species but adds additional flexibility for dealing with the enormity of life history strategies of fishes, which are the most specious group of vertebrate animals on earth. As mentioned above, estuarine fishes exhibit a wide variety of life history strategies, but three endpoints with respect to parental investment and the speed at which
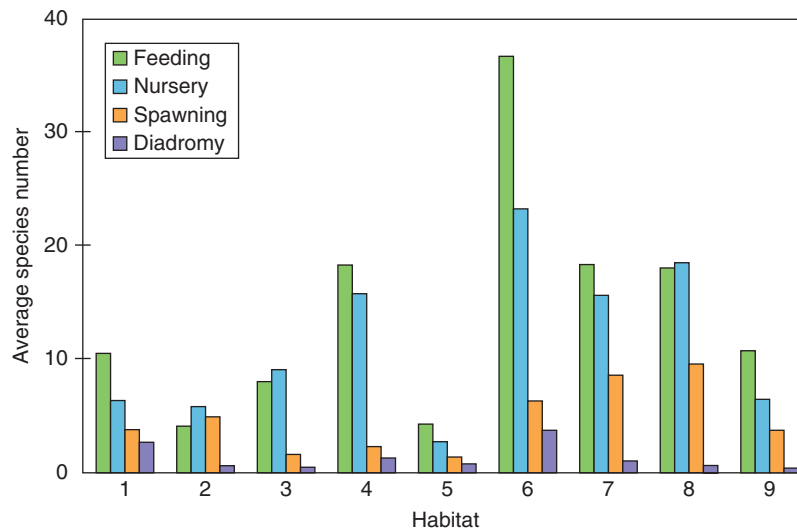
FIGURE 13.3 Relationships between average species number and habitat. *Source:* From Houde (1989).

the life cycle is completed are recognized: (i) opportunistic strategists, (ii) periodic strategists, and (iii) equilibrium strategists.

13.4.2 Life History Strategies and Representative Taxa

Periodic strategists are species that tend to be found in seasonally variable environments or those with large-scale spatial variation. These conditions favor species with large adult size and delayed maturation (long-lived), large clutches of eggs spawned in one or more large batches per year. Periodic strategists generally produce small pelagic eggs that are dispersive but in which there is very little parental investment in each egg. Periodic strategists are ''bet-hedgers'' in that they need only produce strong year classes in some years; in any one year, it is likely that a given female produces no survivors. There are many periodic strategists among the estuarine nekton. These include members of the families Cottidae (sculpins) and their relatives, Gadiidae (cod), Serranidae (basses), Sciaenidae (sea trout, drums, and croakers), Sparidae (sea breams), Pleuronectidae (left-eyed flounders), Chanidae (milkfish), Synodontidae (lizardfish), Belonidae (silver gars), Mugilidae (mullets), Polynemidae (threadfish), Cichlidae (tilapia, freshwater mojarra, and related fish), Tetraodontidae (puffers), Gerreidae (marine mojarras), Leiognathidae (slipmouth, ponyfish), Pomadasyidae (grunts), Pomotomidae (bluefish), Carangidae (jacks), Lutjanidae (snappers), and various families of flatfishes such as the Bothidae (right-eyed flounders), Soleidae (soles), and Cynoglosidae (toungefishes). By and large,

periodic strategists make up the bulk of estuarine transients that spawn offshore, but whose juveniles may be dependent on an estuary as a nursery, or are estuary-related, having juveniles that settle on the portion of the shelf that is influenced by estuarine plumes. Adults of many of these taxa use estuaries as feeding grounds and often consume conspecifics (i.e., they are cannibals).

This list is certainly not complete, and the reader should recognize that the response surface shown in Figure 13.5 is a continuum in which some taxa have traits that are intermediate between the three endpoints. One species that represents the endpoint of the periodic strategy (which is similar to the classic K-selected species) is the striped bass *Morone saxatilis*. This North American species is anadromous and spawns in the tidal freshwaters of large rivers. It can live more than 25 years and begins spawning when 8–9 years old. Mature females can exceed 45 kg and have lifetime fecundity in the many millions of eggs. Striped bass need to produce a strong year class once in only 5–7 years for the population to be long-term stable, and year-class success is related to seasonal and annual variability in river discharge. Young striped bass spend the first few years of their life in an estuary before migrating offshore to join the adult population.

Opportunistic life history strategists are often found in environments that experience stochastic variability on short temporal and small spatial scales. This strategy favors species that mature early and are small and short lived and produce many small batches of eggs over long spawning seasons. As with
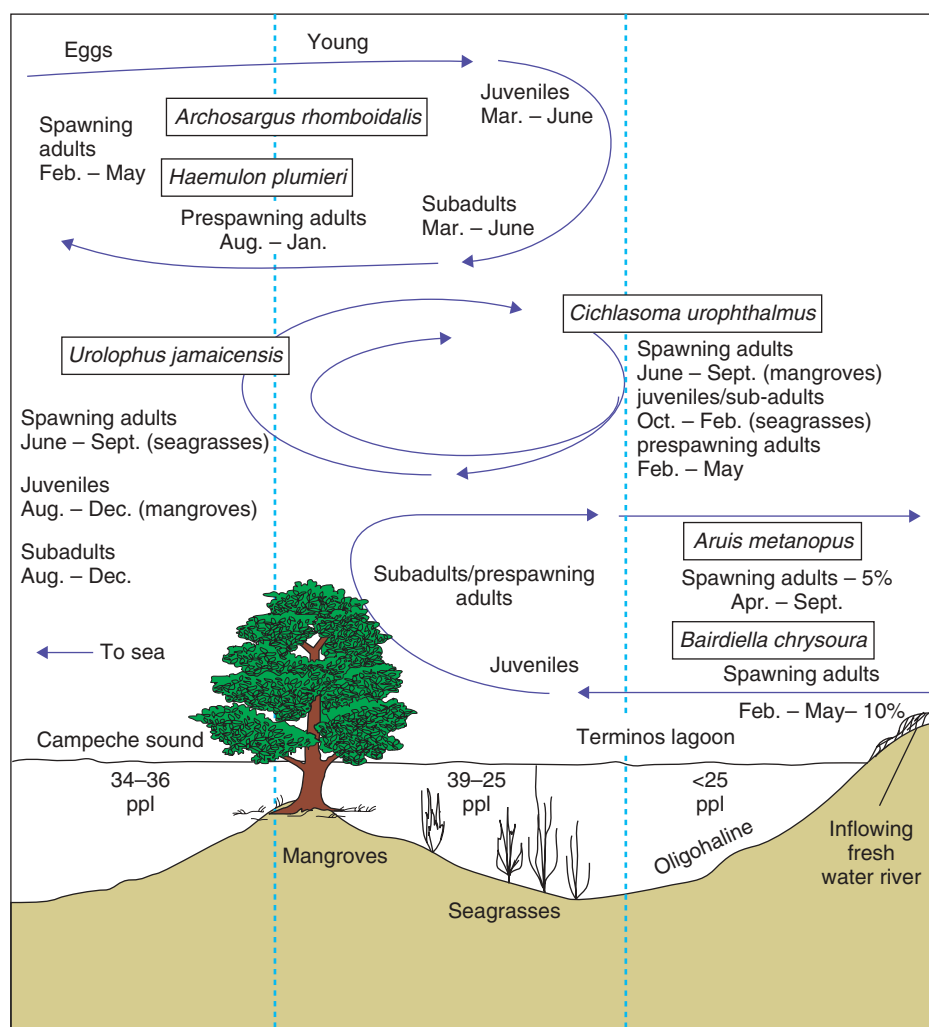
FIGURE 13.4 Life histories of six selected dominant fish species: marine-estuarine spawners *A. rhomboidalis* and *H. plumieri*; estuarine spawners *C. urophthalmus* and *U. jamaicensis*; freshwater-estuarine spewners *A. melanopus* and *B. chrysoura*. The fish migrate using sea grasses/mangroves system (SMS) and fluvial lagoon system (FLS) habitats for the highest periods of productivity for feeding, spawning, or nursery ground. *Source:* From Yáñez-Arancibia et al. (1988, 1993).

periodic stratigists, there is very little maternal investment in an individual egg. These species are much like the classic R-selected species and can quickly recolonize an area in the event of a poor year class. There are fewer opportunistic strategists that use estuaries, but these fishes can be extremely abundant and are frequently important components of the estuarine forage base. Opportunistic strategists include members of families such as Atherinidae (silversides), Clupeidae (herringlike fish), Cyprinodontiodae (killifishes), Engraulidae (anchovies), and Polynemidae (threadfish).

As before, this list is not complete, but one species that represents the opportunistic endpoint is the bay anchovy *Anchoa mitchilli*. This small fish ranges from Massachusetts to Brazil in the Atlantic Ocean and

is frequently among the most abundant fishes in estuaries over its range. Adult bay anchovy seldom reach age 3 and usually weigh less than 5 g. Female bay anchovy can begin to spawn within the first year of life and can spawn more than 100 times during a protracted spawning season, often spawning 50–75 days in succession during peak season. Bay anchovy are referred to as *income breeders* in that egg production is tied directly to feeding rate; it is not uncommon for a female to spawn greater than 400% of her body weight in eggs in a single spawning season, while growing in weight at rates as high as 25% per day. As such, this strategy maximizes the likelihood that some eggs will always be available to take advantage of small-scale variability in conditions that are favorable for survival. Opportunistic strategists such as bay
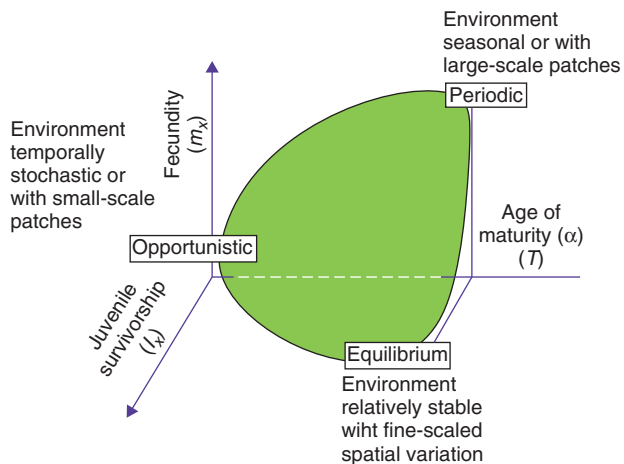
FIGURE 13.5 Trilateral life history continuum of traits that enable nekton to cope with spatially and temporally variable environments. *Source:* From Winemiller and Rose (1992).

FIGURE 13.6 Three-dimensional ofln maturation length, ln mean clutch size, and investment per progeny for 68 marine fishes. Maturation length is the modal length in mm TL, mean clutch size is the mean batch fecundity for a local ecosystem or location and investment/progeny is an index that can range from 0 = no parental care to 8 = extremely long gestation. A value of 4 = lengthy protection by both sexes, etc. *Source:* From Winemiller and Rose (1992).

anchovy can recover quickly from poor year classes due to high intrinsic rates of population growth.

Equilibrium life history strategists tend to be found in resource-limited environments or in very stable environments with limited environmental variability. These conditions favor species of intermediate body size and longevity and those that produce smaller clutches of large eggs. One distinct characteristic of equilibrium strategists is a marked increas in paternal investment in each progeny. This can occur in the form of nest building and guarding, mouth brooding, live bearing, etc. Having large well-developed young means that they are more likely to be competent feeders, or able swimmers, when first born. As such they avoid some of the difficulties faced by less poorly developed eggs and larvae that are associated with variable food resources and local retention within an estuarine ecosystem. Perhaps surprisingly, there are equilibrium strategists that have adapted to living in estuaries. These include members of the families Salmonidae (salmon and trout), Osmeridae (smelts and capelin), Gasterosteidae (stickleblacks), Cottidae (sculpins), and their relatives, Poecillidae (live-bearers and guppies), Ariidae (sea catfishes), Gobiidae (gobies), Syngnathidae (pipefishes and sea horses), and elasmobranchs (sharks, skates, and rays).

Salmon, sticklebacks, sculpins, and gobies build and defend nests, both tasks of which are usually done by males. Smelts and capelins lay their eggs on beaches on the very highest spring tides, and the eggs develop in the sand until the next spring tide when they all hatch on the same night. Sea catfishes are mouth brooders, whereby the males scoop up recently laid eggs in their mouths where they hatch and stay

until the small catfish are fully developed. Sea horse and pipe fish females lay their eggs in a pouch on the males' chest where they hatch and are released as fully capable, albeit small copies of the adults. As such, equilibrium strategists trade fecundity (life egg production) for parental investment, often to the detriment of the adults.

In an examination of North American fishes for which sufficient data were available, Winemiller and Rose (1992) ordinated 68 marine species in a three-dimensional plot with axes labeled maturation size, investment/progeny, and clutch size, which are analogous to the traits of longevity, parental care, and fecundity in the discussions above (Fig. 13.6).

Truly marine species (blue circle) are more likely to fall out toward the periodic corner of the ordination, whereas estuarine species (green circle) can be periodic, opportunistic, and/or have traits that are intermediate between the endpoints. The red circle contains sea catfishes and pipefish, most of which occur in estuaries. Their high parental care makes them fall out toward the equilibrium side of the ordination. What should be clear is that while there are species that fit the endpoints of each strategy, there are many more that have traits that are intermediate between the endpoints. As such, it is not always clear which ecological circumstance favors which strategy, but you can see how variability in estuarine conditions and circulation patterns likely play a role. Undoubtedly, adult life history characteristics have

diverged adaptively in response to environmental diversification and habitat segregation.

Spawning outside estuaries provides the stimulus for evolution of a pelagic larval period for those periodic strategists that are considered to be either ''estuarine dependent'' or ''estuarine related'' such that small egg sizes increase fecundity and prolonged larval periods permit small progeny to accumulate resources by capitalizing on planktonic habitat that is rich in small prey. But for these species, advective losses can be significant and many of the young may never make it to an estuary. In most years, no progeny of any given female survive to maturity.

Rapidly changing environmental conditions within estuaries, and problems related to retention of young within estuarine systems, provide the stimulus for evolution of different life history strategies. Opportunistic strategists evolved to spawn small batches of eggs over long spawning seasons inside estuaries, and equilibrium strategists evolved to produce big eggs with some paternal care that favors retention and to produce larvae capable of feeding immediately after birth. However, opportunistic strategists can exhibit bloom or bust population dynamics given their short life spans, and the equilibrium strategy can be costly to adults, especially if survival is low.

13.5 LIFE AND DEATH IN ESTUARIES

13.5.1 When Is Year Class Success Determined?

It is now accepted that for most estuarine nekton, year-class success is determined during early life through a variety of mechanisms that are not always well understood (Houde, 1989; Pauly and Yáñez-Arancibia, 1994, and see Pauly and Yáñez-Arancibia, this volume). This knowledge is pragmatic rather than mechanistic and is based on the observation that there is little to no correlation between abundance estimates of successive life history stages until the late larval to juvenile stages, after which the number of survivors (often referred to as *recruits*) is correlated to the number of subsequent adult spawners (Fig. 13.7).

This occurs because numbers of eggs and larvae decline exponentially at very high and variable rates, especially those of periodic and opportunistic life history strategists. Eggs and newly hatched larvae often die at rates exceeding 50%/day; these rates may be as high as 95%/day for species such as the bay anchovy. Mortality rates of feeding-stage larvae are
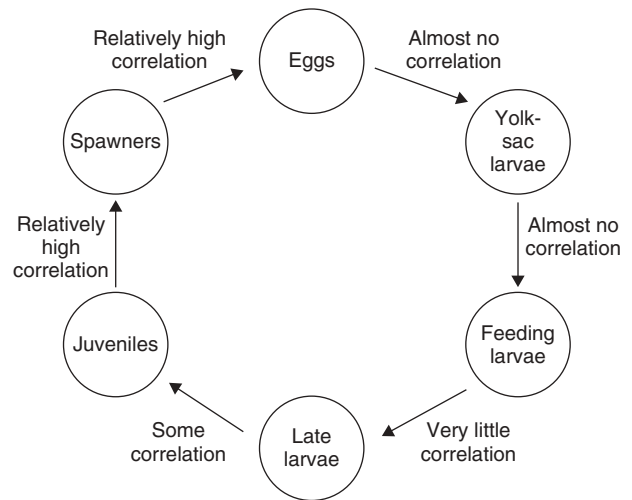
FIGURE 13.7 The relative correlations between successive life history stages of estuarine nekton from eggs to spawning adults. *Source:* From Houde (1989).

lower but can be as high as 30–40%/day. Most of the mortality of early life history stages is attributable to predation.

In fishes, vital (growth and mortality) rates are related and are very plastic, so these rates can differ greatly among seasons or years in response to environmental variability, including food abundance. Unfortunately, growth and mortality rates are related in a way that David Cushing called the *single process*. Cushing (1975) inferred that the longer an individual remains vulnerable to predation, the higher the cumulative mortality rate, which means that slow growth tends to increase the likelihood of being eaten because you do not outgrow your potential predators as quickly as fast growers. Houde (1989) used scenarios presented in Table 13.4 to illustrate how the ''single process'' can result in recruitment successes and failures without invoking episodic population losses.

These results show that relatively small changes in growth (here represented as age to metamorphosis) and mortality rates (here mortality coefficients) can generate order of magnitude and larger variabilities in year-class success. In an estuarine setting, anything that can affect either rate (even subtly) can have a big effect on the number of survivors (recruits), and these rates, especially mortality, are difficult to estimate in the field.

13.5.2 Factors Affecting Growth, Mortality, and Community Structure of Estuarine Nekton

In most cases, less than 50% of the nekton found in estuaries are year-round residents. Observed

TABLE 13.4 One good and three bad recruitment scenarios[a]

Condition	Initial Number in a Cohort	Mortality Coefficient (z, per day)	Age at Metamorphosis (t)	Number of Recruits
Good	1×10^6	0.100	45.0	11,109
Bad-1	1×10^6	0.125	45.0	3,607
Bad-2	1×10^6	0.100	56.2	3,625
Bad-3	1×10^6	0.125	56.2	889

[a]All cohorts initially begin with 1 million larvae. The mortality coefficient is from the formula $N_t = N_0 e^{-(zt)}$, where N_t is the number surviving to age t in days, and N_0 is the initial number of larvae (here 1 million). Age at metamorphosis is the time it takes for larvae to become juveniles (i.e., a low number = fast growth). *Source:* From Houde (1989).

variability in the seasonality of occurrence appears to be created by responses to temperature and salinity, but oxygen levels, habitat, predation, interspecific competition, hydrodynamic processes, and exotic species may also play a role. The seasonal use of estuaries by nekton is very complex. In the following sections, we discuss some of these abiotic and biotic factors in more detail.

13.5.2.1 Abiotic Factors

Salinity has long been hypothesized to be a the main driver of nekton community response in estuaries (Deegan et al. 1986; Evans 1993; Pattillo et al. 1995) becuase of the potential for strong salinity gradients in estuaries. Water temperature also is important, as it affects distribution both between and within estuaries seasonally, although temperature effects also are important and are closely tied to the effects of other variables such as DO. In some estuaries, there are striking differences between summer and winter fish faunas that are likely due to the salinity and temperature tolerances and preferences of different species, as is the latitudinal change in the composition of estuarine faunas along the east and west coasts of the North America. Individual nekton species have salinity and temperature ranges over which they perform best, for example, the gulf menhaden *Brevoortia patronus* is most abundant at temperatures ranging from 25–35 °C, but their distribution is also affected by salinity and food supply.

In temperate and colder regions, the feeding rate of nekton is seasonal. Nekton that do not migrate in winter months often do not feed or feed very little when the water is cold. This behavior is attributable to the energy budget for growth, which is called *bioenergetics*, and is expressed in difference form by the formula:

$$W_t = W_{t-1} + (p * C_{max} * A) - R_{tot}\Delta t \qquad (13.1)$$

where W_t is the weight today, W_{t-1} the weight yesterday, $p * C_{max}$ the proportion of maximum possible food intake realized, A the assimilation efficiency,

R_{tot} the respiration rate, and Δt per unit time, usually 1 day. Respiration is highly dependent on temperature and weight in cold-blooded animals such as fishes and slows down in the winter. This means that in cold conditions, fishes do not need to eat much to maintain their weight or grow, which can be either very low or negligible in winter (Fig. 13.8).

Consequently, resident fishes in temperate estuaries often feed actively in spring and fall, which has to do with recovering from winter conditions in the spring and storing enough energy in fall to prepare for winter conditions, respectively. In general, however, adult fishes must consume 1–30% of their body weight/day at optimal temperatures depending on the level of normal activity. For example, 3% body weight/day is typically required for lurking predators, whereas higher values have been observed for anchovies or other constantly moving filter feeders or planktivores. Feeding rates are much higher for early life history stages (3–50% for juveniles and 50–400%/day for larvae), stressing the importance of food supply on growth rates during early life in the ''single process'' and recruitment variability.

Salinity also exercises strong control over the distribution and physiology (via osmoregulatory requirements) of fishes within estuaries. Intermediate and fluctuating salinities keep species diversity low. Species diversity is minimal when salinities range from 3 to 8 ppt. This is referred to by some as the salinity *no man's land* as it excludes many truly marine and freshwater species. That said, mobile ''estuarine'' nekton species usually are capable of living in a wide range of salinities, but will respond by moving into a preferred range that is species specific (Table 13.5).

Often, different life history stages have different salinity preferences and may differ in their ability to survive salinity changes. Young fishes tend to be more stenohaline than adults, undoubtedly due to poorly developed osmoregulatory systems, or may starve or be eaten by predators if growth slows when flushed into less productive regions by high flows. Unusually
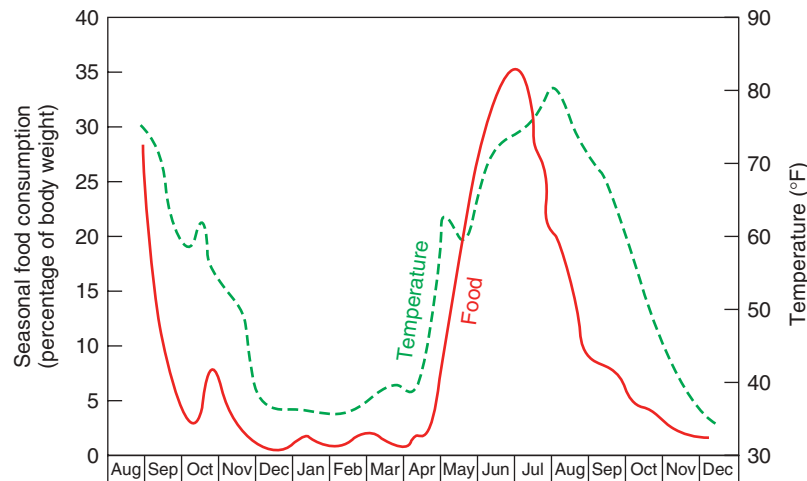
FIGURE 13.8 The relationship between seasonal food consumption by a fish species and water temperature in a temperate reservoir.

TABLE 13.5 Distribution of common fishes in the Navarro River and its estuary, California, in relation to salinity

Species	Salinity (ppt) Classification[a]	O[b]	O[c]	1	3	9 to 10	23 to 25	30+
Sacramento sucker	1	X[e]	X	X	—	—	—	—
California roach	1	X	X	X	X	—	—	—
Prickly sculpin	2	X	X	X	X	X	X	X
Rainbow trout	3	X	X	X	X	X	X	R
Threespine stickleback	2 and 3	X	X	X	X	X	X	X
Starry founder	4	—	X*	X*	X*	X*	X	X
Shiner perch	4	—	—	R*	R*	X*	X	X
Jacksmelt	4	—	—	—	R*	X*	X	X
Bay pipefish	4	—	—	—	—	X	X	X
Plainfin midshipman	4[d]	—	—	—	—	X	X	X
Penpoint gunnel	4	—	—	—	—	—	X	X
Pacific herring	4[d]	—	—	—	—	—	X	X
Surf smelt	4	—	—	—	—	—	X*	X
Northern anchovy	4	—	—	—	—	—	X	X
Lingcod	5	—	—	—	—	—	—	X*

[a]The species are classified according to their salinity tolerance as follows: 1, stenohaline, freshwater; 2, euryhaline, freshwater; 3, anadromous; 4, euryhaline, marine; and 5, stenohaline, marine.
[b]More than 1 km upstream from first riffle.
[c]Just above first riffle.
[d]Spawning.
[e]Indicates that the fish were present and common, R that were present but rare.
*Indicates predominantly young-of-year fish.

high salinity can also affect nursery function, particularly in arid regions. Estuaries that are deprived of freshwater become more saline, and thus have reduced capacity to support ''estuarine-dependent'' nekton species. The numbers of marine predators in estuaries often increase dramatically during drought conditions because of high salinity conditions.

DO is another abiotic factor that is highly variable in estuaries. Problems can arise during periods of low flow, especially when natural levels of organic inputs remain high. Problems also arise when flows are high and anthropogenic inputs of inorganic nutrients overstimulate primary production (i.e., eutrophication), which when coupled with stratification of the water column can cause hypoxia or anoxia. One newly emerging problem associated with eutrophication and hypoxia in estuaries is the increase in gelatinous zooplankton. These animals are more tolerant of low

DO than many nekton species (particularly nekton early life history stages) and voraciously consume both zooplankton and fish eggs and larvae. Moreover, gelatinous zooplankton themselves are rarely preyed on directly and are thus a trophic dead end in the estuarine food web.

Hydrodynamics and wind stress can also affect recruitment in estuarine ecosystems. Hydrological conditions and coastal morphology can determine the amount of potential settlers, as many estuary-dependent and estuary-related species spawn offshore and rely on currents to transport them inshore and demersal nekton often prefer to settle from the plankton on specific bottom types. Once in an estuary, strong residual currents favor retention, but asymmetric tidal currents can be a problem. For example, many of the world's estuaries have tidal currents that are generated astronomically, but others occur in microtidal environments where currents are generated by meteorological events and are less predictable in time and amplitude. This dichotomy provides an interesting area of research because transport and retention often involves behaviorally mediated use of tidal circulations, but some estuary-dependent nekton species are equally as successful in estuaries that are governed by astronomical tides and exhibit strong two-layered circulations and in estuaries where neither of these conditions persists.

13.5.2.2 Biotic Factors

Although food in estuaries is usually abundant overall, availability of any particular food can show considerable short-term fluctuations. While starvation is rare, the indirect effects of food availability on recruitment via changes in growth rate is high (remember the ''single process''). As such, most estuarine species are not specialized feeders, even though each species or life history stage will show a preference for some general type of food. Hence, feeding is strongly tied to habitat type (Vega-Cendejas et al., 1994; Rivera-Arriaga et al., 2003; Yáñez-Arancibia et al., 2007). Sooner or later, almost every potential source of energy will will be consumed by something (nekton or otherwise), and at any given time, it is unlikely that any significant source of food will be underutilized. Remember, estuarine food webs are simple and the number of species that are abundant at any one time is likely to be low, especially in cold temperate and boreal estuaries, but often are complex with a number of dominant second-order consumers in warm and tropical estuaries (Deegan and Thompson, 1985; Christensen and Pauly, 1993; Vega-Cendejas et al., 1994; Yáñez-Arancibia et al., 1994).

While not overly specialized, there is much diversity in the diets of estuarine nekton. Food sources range from nutrients in solution to plants (micro and macro) and animals (micro to macro). The observed diversity in diets is due to diversity in habitat and body form. Some nekton species are exclusively herbivorous or carnivorous but most are omnivores and generalists, that is, a variety of food types are eaten in the same order of abundance in which they are encountered (feed nonselectively). Other species are exclusively parasitic. Most nekton species also experience significant changes in diet with ontogeny, and the life cycles of fishes are often tied to cycles in food abundance. The bottom line is that fishes are strongly tied to their environment via food webs, and the diversity of habitats and body forms results in a diversity of feeding types. While it is difficult to generalize the diversity of feeding types, one broad characteristic prevails. Namely, food is ingested through the mouth; other than that almost anything goes, but certain broad categories are recognized. These categories include the following.

Predators. Predatory nekton feed on macroscopic animals using well-developed grasping, cutting, or holding teeth. A rule of thumb is that any nekton species that catches and consumes prey that is $\geq 1/3$ of its own body length is considered a predator. Many predators actively hunt for prey (e.g., bluefish *Pomatomus saltitrix*), others lurk (winter flounder *Pseudoplueronectus americanus*), and others use lures (monkfish *Lophius americanus*). Depending on how they obtain their prey, some hunt by sight (e.g., bluefish), while others use smell (blue crabs *Callinectes* sp.), sound, and mechanoreception (sharks and rays) or touch (e.g., northern stargazer *Astroscopus guttatus*).

Grazers. Grazing nekton take food in bites, often by small individual bites. In estuaries, grazers often browse on micro- and macrovegatation, the latter being much like ruminants (e.g., mullets family, Mugilidae, which have gizzards for grinding plant material). Biters of animal prey also are included among the grazers (e.g., pinfish *Lagodon rhomboides*), and as such can be difficult to distinguish from predators other than the predator to prey size ratio discussed earlier.

Strainers or filter feeders. These species strain or filter small organisms from the water column and food items are selected by size rather than by kind. Many consume phytoplankton using adaptations in the mouth and jaw that facilitate the collecting and

swallowing of a concentrated ''bollus'' of millions of cells at a time. This type of feeding is very important in the clupeiods (herringlike fishes and their relatives); for example, gulf menhaden use gill rakers to filter the water column and can filter 5–10 $1/m^{-1}$, removing all but the smallest phytoplankton from the water. Strainers and filter feeders feed near the base of the food webs and often are found in estuaries in very high biomass, which makes them part of the forage base for nekton that feed at higher trophic levels.

Suckers. These species suck food into the mouth or ingest food-containing material such as bottom substrate. Suckers are mostly bottom feeders that usually have inferior mouths and modified lips (e.g., Gobiidae, Eliotridae, and Ariidae). The most important feeding stimuli for suckers is the sense of touch, so many species have barbels around the mouth that contain taste buds. Many suckers are detritivores that take in mouthfuls of sediment and clean it of food, then spit out or excrete the unusable material. Some of the estuarine drums and croakers (Sciaenidae) feed as described above and use barbels to search for benthic prey in soft sediments. Others have lips modified for scraping or rasping and can remove food from hard surfaces (Gerreidae). For example, mullets (Mugilidae) can scrape macrovegetation from rocks and shells and can also feed on macrovegetation such as *Ulva* sp. and are thus grazers.

Parasites. parasitic nekton share one the most highly evolved feeding habits among animals of the world. The best example of an estuarine parasitic nekton species may be the anadromous sea lamprey *Petromyzon marinus* that cuts or scrapes holes in the sides of larger nektonic hosts, from which they drink blood and body fluids.

Now that we have briefly discussed feeding types, we can make a transition to discuss some of the biotic factors that affect recruitment and structure estuarine nekton communities. It will quickly become apparent how these subjects relate.

13.5.2.3 Biotic Factors and Community Structure

Predation is one of the most important factors regulating recruitment success and community structure in estuaries because many transient species are predators as adults, and these can occur in large numbers. Hence, the impact of predation on both invertebrates and fish populations can be large (i.e., top-down control of abundance). Large concentrations of predators can locally deplete prey populations and become food-limited (e.g., demersal fishes feeding on benthic invertebrates are believed to be responsible for low densities and biomass in subtidal soft substrate habitats), but predators consumption often are offset by high $P : B$ ratios of prey. Young nekton using estuaries as nursery areas are also subject to intense predation (remember the refuge hypothesis?), but mortality rates of the juveniles may be compensated for by rapid growth rates (the single process again). Rapid growth enables them to quickly out grow many types of predators (Pope et al., 1994). In general, other sources of abiotic and biotic variability (i.e., density-independent regulation) are more important than predation in structuring estuarine prey and/or nekton communities.

Before we move on, this is a good time to introduce a very important topic concerning population regulation. Food-limited growth is a common phenomenon in most estuarine ecosystems, and it is rare to observe estuarine nekton growing at their maximum potential rates. However, as mentioned earlier, food limitation is most often driven by factors other than intraspecific consumption of prey resources. However, it is also true that the nekton populations in nature do not grow to infinite size because at some point, population growth becomes limited by some resource. When intraspecific competition for food or space does become limiting, this feedback is considered density dependent rather than density independent. Density-dependent population regulation in part explains why it is possible to exploit populations sustainably.

Competition, such as predation, does not seem to be as important as environmental fluctuations in regulating the abundance and community structure of estuarine nekton. Most studies on food habits of estuarine nekton show a high degree of overlap in diet among the species present, which is probably due the low number of species of abundant invertebrate prey in estuarine soft bottoms. Nevertheless, it has been argued that the staggered use of estuaries by estuary-dependent nekton may be, at least partially, a mechanism for the species to reduce interspecific competition for food by their young (Fig. 13.9).

For example, juvenile sciaenids (e.g., Atlantic croaker, *Micropogonias undulatus*, and spot *Leiostomus xanthurus* in Fig. 13.9) manage to segregate partially in estuaries by feeding habits owing to differences in body shape and mouth structure and partially on the basis of distribution and timing of the use (seasonality) of estuaries (Fig. 13.10).

Invasions by nonnative species are a growing problem in estuaries worldwide. Invasive species get introduced mostly through dumping of ballast water
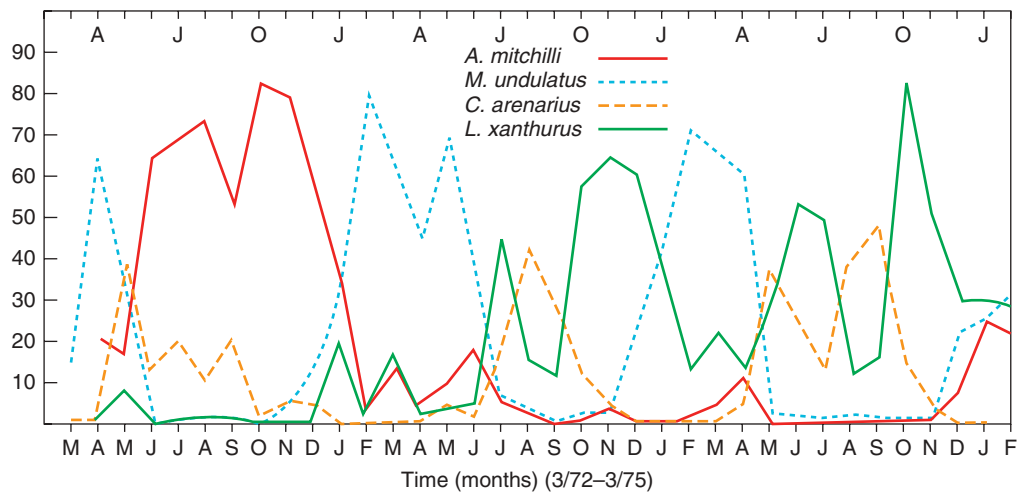
FIGURE 13.9 Relative importance (percent of total caught) of four species of estuarine fishes at different times of year in the Apalachicola Bay estuarine system. *Source:* From Livingston et al. (1985).
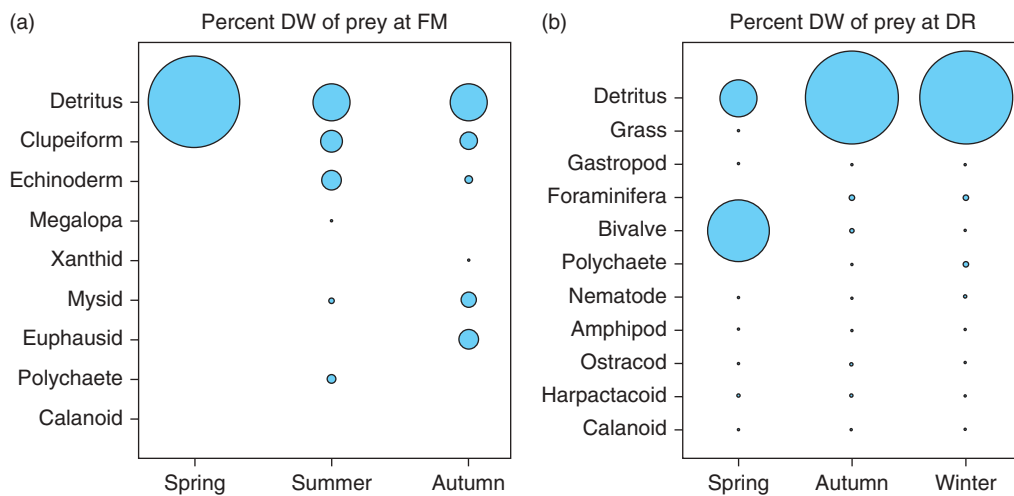
FIGURE 13.10 Diets of juvenile sciaenids in Mobile Bay, AL, collected during the same seasons, but at different locations in the Bay. (a) The percent composition by dry weight (DW) of items to the diet of Atlantic croaker and (b) for spot. The bubbles sum to 100% for each of diet. DR is a region of the mid-bay where spot were much more abundant than croaker. FM is a region in the lower bay where the inverse was true. Samples were collected contemporaneously.

by ships, by unintentional releases from aquaculture, and the aquarium trade has also been implicated. Perhaps, the extreme example in the United States of an invaded estuary is the Sacramento-San Joaquin estuary (San Francisco Bay) of California. Several new species successfully invade there each year and much of the biota is now exotic. One species of note is the striped bass, which is native to the east and Gulf of Mexico coasts of the United States. This species was intentionally introduced in the 1850s and has thrived,

ultimately growing to support a substantial recreational fishery. But as often happens, the striped bass in now considered a pest because it consumes salmon smolts, some species of which are now endangered. Other significant introductions include an Asian clam, whose filter feeding has greatly reduced populations of zooplankton required as food by larval fishes, and of the copepod *Sinocalanus* sp., which has replaced the native copepod *Eurytemora* sp., but whose behavior makes it much more difficult for the larvae of native

TABLE 13.6 Relative areas and contributions (percent) to production and potential fish harvests of estuaries, shelf, coastal upwelling, and oceanic ecosystems

Region	Area	Primary Production	Global Fish Production	Potential Global Fish Catch
Estuaries	0.5	2.6	5.2	5.9
Shelves	6.4	15.3	26.2	22.3
Upwelling	1.4	4.6	8.5	8.1
Oceanic	91.7	77.5	60.1	63.7

fishes to catch and eat. The result is a highly altered ecosystem with many endangered native species.

13.6 ESTUARINE FISHERIES

A number of investigations have demonstrated relationships between fisheries yields and the high nutrient loads, freshwater inputs, shallow depths, large areas of tidal mixing, coastal vegetated area, surface area of lagoon–estuarine systems, and resulting high productivities that are typical of estuaries and estuarine plume ecosystems (Pauly and Yáñez-Arancibia, 1994, 2011, this volume; Cowan et al., 2008; Sánchez-Gil et al., 2008; Baltz and Yáñez-Arancibia, 2011). Because of these relationships, and despite the small aggregate spatial extent of estuaries (<1% of the global marine area), almost 6% of fishery yields have historically been derived from estuarine or estuary-dependent species (Table 13.6).

In the US Gulf of Mexico, the fraction is considerably higher; estuary-dependent species dominate in large and valuable commercial and recreational catches. For example, gulf menhaden, *B. patronus*, support the second largest US fishery by weight, and peneid shrimps support the fifth largest by value; shrimp landings alone are valued at $400–500 million/year. Additional information on estuarine and coastal fisheries can be found in the studies by Mann (2000) and Baltz and Yáñez-Arancibia (2011) and Chapter 18 of this volume.

Fish production in estuaries and in coastal ecosystems is governed by the laws of trophic supply and demand, and changes in nutrient supply for primary producers can filter up through the food web to fishes, thereby increasing fish production if overall production is increased at lower trophic levels. Moreover, we have already learned that estuaries serve as nursery areas for fishes that spawn offshore, enter estuaries as larvae and/or juvenile, and after a period of residency, move back offshore to complete their life cycles. While in estuaries, larvae and juveniles are abundant and often experience phenomenal growth rates and biomass production that result from very high feeding rates, but factors that affect abundances of young fishes in estuaries are not well known, especially in the tropics, and many factors identified as important to fisheries production in more comprehensively studied, temperate estuaries clearly are not universal. That said, many of these estuary-dependent species support valuable recreational and commercial fisheries and are derived from highly productive estuaries that seem to share some characteristics such as high river discharge rates, large freshwater surpluses, and low water residence times. Under these circumstances, however, it is possible that much of the production and subsequent trophic transfer may occur outside the physical boundaries of the estuaries, that is, in association with plumes of fresh water over shallow continental shelves. These contrasting sources of trophic delivery to the fishery forage base (estuary and shelf) introduce uncertainty in how we view the functions of estuaries and the shelf ecosystems they influence, especially in the tropics and subtropics. At the very least, we believe that high fisheries production may be attributable in part to estuarine-like conditions that cover large portions of the inner continental shelf during high river discharge periods, because relatively few fish species are wholly adapted to life cycles within estuarine ecosystems. Disentangling the relative contributions to fish production by estuarine and estuarinelike inner shelf ecosystems may be essential for long-term ecosystems-based management of estuaries, especially in light of rapidly changing conditions due to anthropogenic and natural stressors (Baltz and Yáñez-Arancibia, 2011). As a result, understanding ecosystem function (including fishery ecosystems) may be a moving target, as large-scale and rapid changes in fish habitat (some of which are human induced) occur against the backdrop of longer term changes attributable to a variety of human-caused insults, climate change, and loss of coastal wetlands, sea grasses, and biogenic reefs.

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CHAPTER FOURTEEN

THE ECOLOGY OF ESTUARINE WILDLIFE

Russell Greenberg

Protected from the open ocean, gentle meeting places of marine, terrestrial, and riverine ecosystems, estuaries and their many habitats provide a home for a great diversity and abundance of wildlife species. From open embayments to broad expanses of tidal mudflat and the greenery of tidal marshes and mangrove swamps, birds, mammals, reptiles, and a few amphibians live their lives or visit to take advantage of an abundance of food as they move along the coast. This chapter explores the diversity of wildlife in estuaries, the patterns of wildlife abundance in time and space, the ecological role of wildlife in estuarine ecosystems, and how the activities of wildlife and humans influence each other.

14.1 DIVERSITY, EVOLUTION, AND ENDEMISM

14.1.1 Patterns of Diversity

Birds are the most diverse group of terrestrial vertebrates associated with estuaries. Approximately 165 species of North American birds are found commonly in estuaries in at least a portion of their range during some time of the year. Of these, about one-third are coastal species that primarily forage in deeper waters and are also found close to the shore along non-estuarine coastlines. Another third are shorebirds and waders that feed on mudflats, beaches, and adjacent shallow waters. Twenty-five species (mostly waterfowl) are associated predominantly with shallow waters of sloughs and lagoons, and 35 species find their primary home in marshes. The dominant taxonomic groups occupying estuaries are Charadriiformes (shorebirds, gulls, and terns) with 60 species, Anseriformes (waterfowl) 31 species, Passeriformes 21 species, and Ciconiiformes 14 species. Most of the species are found in a variety of coastal or interior wetland habitats and only a handful can be considered specialists, with populations that are largely restricted to coastal estuaries.

Although South America has over three times the total number of bird species than North America (over 3000 compared to 800 regular species), the richness of the estuarine avifauna is only slightly higher. If we exclude the 80 or so species associated with tropical mangrove forests from consideration (Stotz et al., 1996), then the number of estuarine species in South America is actually lower than that in North America (approximately 120 vs 165 species). The largest difference is in the number of species associated with the deeper water of embayments, with only about half the number of species in North America, as well as waterfowl associated with shallow water. The major groups that show lower diversity in South America are diving piscivores (such as loons and grebes) and

diving invertebrate feeders (sea and diving ducks). Estuaries in South America are largely devoid of migrants from high-latitude boreal forest or tundra-breeding areas, which is not surprising considering that the austral migration system is much less diverse than the boreal migration system. This difference in diversity is in part due to the lack of land mass at high latitudes. Although the statistics presented here are for New World estuaries, the general latitudinal patterns apply to Old World estuaries as well.

The diversity of estuarine mammals is considerably lower than that of birds. Of the 400 species of North American mammals, approximately 50 species are regularly found in estuarine habitats (Greenberg and Maldonado, 2006). For mammals, the preponderance is associated with tidal marshes (35 species) with a small number of coastal marine mammals occurring in the open waters. The diversity of tidal marsh mammals is lower in South America (26 species) and still lower in Europe (15 species). Once again, these numbers are augmented by a few species of cetaceans, sirenids, and mustelids (otters) so that a value of 25–50 species of estuarine mammals can be found on any of these continents.

Terrestrial mammals are dominated by small species, particularly rodents in the family Muridae and shrews (in the Northern Hemisphere), augmented by some mid-sized omnivores and carnivores. Marine mammals of estuaries include some whales (found regularly in only a few estuaries) and smaller cetaceans, a few species of seals and sea lions, otters, and, in tropical areas, several members of the dugong/manatee order.

Heatwole (1999) estimated that only 1.4% of the 5300 species of reptiles have made incursions into coastal saline habitats, a vast majority (approximately 70 species) of which is snakes. Few of the over 80 species of saltwater-tolerant reptiles can be found in the open water of estuaries. Habitat associations are known for about half of the marine species of snake. Of these, 14 species are associated with open estuary or mangrove habitats in southern Asia and four are found in salt marshes in North America. Only a few species of turtle (including three species of the sea turtles) make regular use of estuarine habitat, and all but one are found in tropical estuaries (Ernst and Barbour, 1989). Finally, several species of crocodiles are dominant predators in subtopical estuaries.

We have briefly examined the major taxonomic groups found in different estuaries, but estuaries themselves are a composite of interconnected habitats. Each estuarine zone supports a unique assemblage of wildlife taxa, which is explored in Table 14.1.

14.1.2 Functional Diversity

Although species diversity is often not remarkable for vertebrates in estuarine systems, the functional diversity, as reflected in the range of body plans and specialized feeding adaptations, is higher than in most ecosystems. The range of body sizes provides prima fasciae evidence of high functional diversity. The size range in estuarine mammals dwarfs that of other vertebrates ranging from shrews (5 g) to small baleen whales (45,000 kg) and includes most of the major orders and foraging guilds. Birds of estuaries range from among the smallest (humming birds in mangrove swamps and wrens in salt marshes) to among the largest volant bird species, including the dalmation pelican (*Pelicanus crispus*, 9 kg) of Eurasia. Similarly, among reptiles, the estuarine fauna includes all of the major morphotypes including snakes, lizards, turtles (including sea turtles), and crocodiles. They range in size from small snakes and lizards up to the largest living reptile, the estuarine crocodile.

With the local diversity of habitats, from marsh vegetation and mudflats to shallow and deep waters, it is likely that no other ecosystem supports as great a diversity of foraging opportunities and challenges as estuaries. The behavior and morphological design of birds, in particular, show profound variation as shown in Table 14.2 and Figure 14.1. What follows is a brief overview of some of the behavioral and morphological adaptations that can be found among birds feeding only tens of meters apart along an estuarine shore.

14.1.3 Endemism in Estuarine Faunas

For the most part, vertebrate species that occupy open water habitats in estuaries have a broader coastal distribution and are undifferentiated in estuaries. One notable exception may be found in bottlenose dolphins, and perhaps other small cetaceans. Along several coastlines, pelagic and inshore bottlenose dolphins comprise morphologically differentiated ecotypes that reflect distinct lineages based on the analysis of mitochondrial DNA (Hoelzel et al., 1998).

Species found in the shallow water, mudflat, marsh, and mangrove habitats are usually widespread in freshwater wetlands or even other forest or grassland habitats, but at times are represented in estuarine habitats by different species or differentiated populations within a species. Endemism in particular habitats is shaped by the difference in selective environments between estuaries and adjacent habitats. Of all of the estuarine habitats, it is

likely that salt marsh and mangroves are the two that provide the strongest environmental discontinuity. Features of tidal marshes and swamps that might shape local adaptation include salinity, tidal flux, and the simple floristics and vegetative structure. Countering the forces of locally divergent environments, marshes and swamps are often not very extensive and not separated from interior wetlands and grasslands, and are unstable in extent and distribution through time (Malamud-Roam et al., 2005).

Local divergence has been documented for populations of at least 25 species of salt marsh vertebrates,

TABLE 14.1 **Foraging behavior and adaptations in estuarine birds**

Foraging behavior	Description	Adaptation	Examples	References
Foliage gleaning	Move through dense vegetation using small, often thin bills for prey capture and probing	Short, thin bill (except sparrows which also probe and eat seeds)	Wrens, sparrows, warblers, spinetails	
Cursorial surface picking	Largely visual. Short bills are used to pick invertebrates off the surface	Short- to medium-length bill	Plovers, sandpipers	Nebel et al. (2005)
Tactile mud probing	Probe into the substrate; sometimes with a sewing-machine-like motion where the long bill is rapidly inserted through shallow water and into the substrate below to locate and capture prey	Long, narrow bill with a small sensory organ (Herbst Corpuscles) near the tip of the bill. Bill curvature is assumed to increase the effective volume of substrate processed tactilely per unit time	Sandpipers, dowitchers	Nebel et al. (2005)
Burrow probing	Probe burrows of crabs and other large invertebrates	Long, down-curved bills with bill lengths of over 180 cm in some species	Curlews	
Secretive marsh probing	Probe in mud in dense vegetation	Long, narrow bill; lateral compression of skeleton for movement in narrow spaces	Rails	
Vortex spinning	Spinning, their dabbling feet creating a small vortex in the water, small invertebrates can be picked off the surface and suspended by the vortex surface	Moderately long, straight narrow bill; lobed feet	Phalaropes	Rubega and Obst (1993)
Shallow water ploughing and sweeping	Ploughing motion of its bill to disturb and capture its prey; slow sweeping motion or rapid sweeping while running through the water	Broad, deep bill or bill with broad spatulate tip that is well endowed with sensory papillae	Spoonbills, spoon-billed sandpiper, boat-billed heron, avocets	

(*continued*)

TABLE 14.1 (*Continued*)

Foraging behavior	Description	Adaptation	Examples	References
Wading and fish spearing	Wade in shallow water, often employing a sit-and-wait strategy for capturing fish. Species in the genus *Buteroides* (e.g., green-backed herons) are widely reported to drop bait on the water surface to attract fish. Other species employ a variety of tactics to flush or attract prey including shuffling their feet or spreading their wings to form a shaded canopy	Long, spear-shaped bills; long legs	Herons and egrets	Lovell (1958), Kushlan (1981)
Filter feeding	Flamingos (*Phoenicopterus*) wade in shallow water. The head is inverted so the upper mandible is held below the lower mandible. The inverted banana-shaped bill is fringed with laminae, which filter water for small prey	In the flamingos, the thick tongue is thrust back to pump water in and then forward and sideways to press water through the sides of the bill where the filter retain prey of 4–8 mm. The spacing of the laminae is finer toward the tip of the bill, so the flamingo can adjust the mesh of the filter it is using—presumably to the size of the plankton on which it is foraging, by manipulating water along the beak	Flamingos	Zweers et al. (1995).
Grazing and dabbling	Graze terrestrial plants and forage on submerged aquatic vegetation by tipping over and reaching down	Broad, strong bills. While most of the bill is flexible, the nail at the bill tip is hard and allows for a firm grasp. The bills of grazing geese have sharp edges for clipping vegetation, whereas many species of ducks have laminae fringing, which allows the sieving of water for small prey and food particles.	Waterfowl	

TABLE 14.1 (*Continued*)

Foraging behavior	Description	Adaptation	Examples	References
Surface diving	Fish and invertebrates below the surface or attached to the bottom substrate are often harvested by birds that swim on the surface and dive	Birds are propelled under water by paddling their webbed or lobbed-toed feet or with their wings. Adaptations for diving include having legs and feet far back on their body and large feet for power kicking under water. Diving ducks often stroke simultaneously with both feet in a dolphin kick. Air stored in air sacks is rapidly expelled and feathers flattened to increase ballast and make diving easier. Diving birds that feed primarily on fish or shrimp have long narrow bills, which reduce water resistance and close quickly around prey. Bill edges, the palate, or tongue may have recurved teeth for grasping slippery prey. Alternatively, the tip of the bill might be hooked (as in cormorants). Diving and sea ducks feed primarily on shellfish and use their broad, heavy duck bill to pull or pry their prey from the surface.	Loons, grebes, cormorants, ducks.	
Plunge diving	Fish can be spotted by birds flying over the estuary and captured by plunge dives to the surface, either by the bill (terns, gulls) or feet (ospreys, Pandionidae).	Since perches are rare over estuarine waters, most plunge diving species are adept at hovering in one place to facilitate searching for schools of fish. Birds that capture fish with their bill often have long, narrow, daggerlike bills that pierce the water easily and close quickly around fast-swimming prey. Similarly, osprey feet have a reversible front toe and small barbs to help hold onto fish.	Terns, kingfishers, osprey	Ashmole (1968)
Aerial piracy	Kleptoparastisim involves the stealing of prey captured by one animal by another animal. Occurs opportunistically in many species.	Powerful flight and large body size	Jaegers, eagles, gulls, frigate birds	Furness (1987) Grant (1971)
Carrion and detritus feeding	Locate, dominate, and feed off scattered animal carcasses and organic garbage	Olfactory and visual acuity, large home range, ability to garner social information on food sources, and specialized adaptations, such as the ability to detoxify certain compounds associated with the rotting of biological substances.	Corvids, gulls, vultures, caracaras, bald eagle	DeVault et al. (2003)

TABLE 14.2 Characteristic wildlife species in different estuarine zones

Estuarine zone	Birds	Mammals	Reptiles and amphibians
Outer bays	Gulls (*Laridae*), terns (*Sternidae*), cormorants (*Phalacrocoracidae*), pelicans (*Pelicanidae*), diving ducks (*Aythyinae*) sea ducks (*Merginae*), loons (*Gaviidae*), and grebes (*Podicepiidae*).	Humpback (*Megaptera novaeangliae*), minke (*Balaenoptera acutorostrata*), gray (*Eschrichtius robustus*), pilot (*Globicephala* spp.), orca (*Orcinus orca*), and beluga whales (*Delphinapterus leucas*). Inshore species of small cetaceans include over a dozen species of dolphins and porpoises of the neritic coastal zone, harbor seals (*Phoca vitulina*) and occasionally other species of seals (*Phocids*) sea otters.	Diamondback terrapin, sea turtles, sea snakes
Shallow waters, inner bays, river mouths	Gulls, terns, cormorants, pelicans, diving ducks and grebes	Dugongs and manatees (*Sirenidae*), and otters	Crocodiles, some turtles
Sandy beaches	Gull, terns, shorebirds	Seals and sea lions	Breeding sea turtles and terrapins
Mudflats	Shorebirds, wading birds	Harbor seals	
Salt marsh	Passerines such as pipits and wagtails, wrens, sylviid warblers, emberizid sparrows, rails, herons, egrets, and other wading birds, terns and shorebirds.	A variety of rodents (e.g., voles, mice, rats, nutria, muskrats), and shrews along with variety of mid-sized omnivorous and carnivorous species including raccoons, opossums, small canids, and cats. Large herbivores include deer and domestic livestock.	Saltmarsh snakes (*Nerodia*), diamondback terrapins
Fresh and brackish marsh	Similar birds to those found in salt marshes, but more diverse including a number of songbird species associated with any interior freshwater marsh systems. In Europe and Asia, these areas are often dominated by the common reed (*Phragmites australis*) and support reed-inhabiting warblers (*Acrocephalus* spp.), buntings, and tits.	Similar mammals to those found in salt marshes, but with greater diversity. Muskrats and deer can be common.	Most of the non-specialized reptile and amphibian species that inhabit estuarine waters.
Mangroves	Herons, bitterns, cormorants, kingfishers, buteos. Important canopy birds include hummingbirds in the New World and sunbirds, flower eaters and honey eaters in the Old World. Insectivorous passerines (woodcreepers, flycatchers, vireos, wood warblers, old world warblers, white-eyes, and tanagers), bee-eaters, woodpeckers, and pigeons.	Leaf (*Prebytis cristatus*) and proboscis monkeys (*Nasalis larvatus*) in southeast Asia and howler monkeys (*Allouatta* spp.) in the New World. Large Asian and Australian fruit bats known as flying foxes (*Pteropus* spp.). Hammerhead bats in Africa form large roosts in the canopy of mangrove swamps. Otters and fishing cats.	Crab-eating frog (*Fejervarya cancrivora*), crocodiles, a few turtles, and snakes.

(a)

(b)
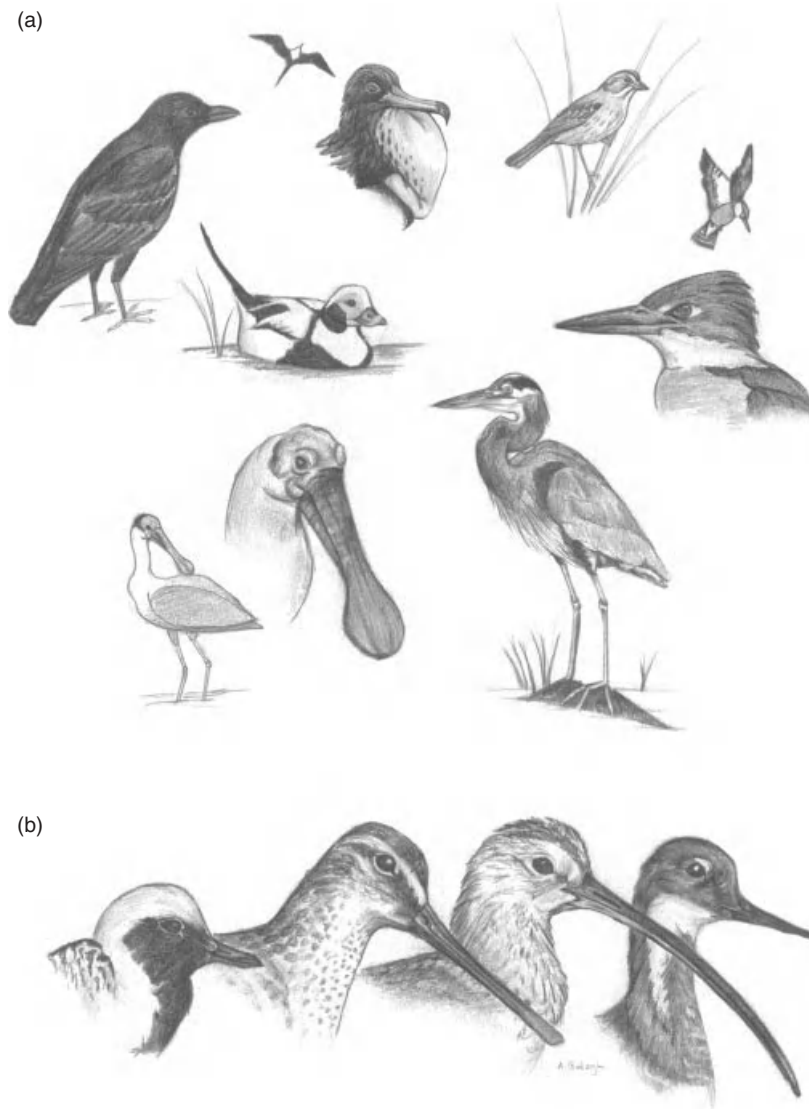
FIGURE 14.1 With their diverse and often highly productive habitats, estuaries support a very high level of functional diversity. Here we illustrate some of the morphological variation in adaptations for foraging among birds (See Table 14.2 for descriptions of adaptations): (a) (clockwise from top center) magnificent frigatebird (*Fregata magnificens*), an aerial pirate; seaside sparrow (*Ammodramus maritimus*) a marsh insectivore–granivore; ringed kingfisher (*Ceryle torquata*) a plunge diver, great blue heron (*Ardea herodias*) a wading piscivore, roseate spoonbill (*Platalea ajaja*) a wading filter feeder; long-tailed Duck (*Clangula hyemalis*), and American crow (*Corvus brachyrhynchos*) a scavenger; (b) Three species of scolopacid shorebirds with different bills for foraging for invertebrates at different depths of water or mudflat, black-bellied plover (*Pluvialis squatarola*); long-billed dowitcher (*Limnodromus griseus*); and long-billed curlew (*Numenius americanus*).

primarily in North America (Greenberg et al., 2006). Almost all of the endemic taxa are subspecies. The mangrove fauna is both more diverse and more poorly known than that of salt marshes, but 63 taxa (44 species and 19 subspecies) terrestrial vertebrate species have been reported to be either endemic to mangroves or have recognized subspecies restricted primarily to mangroves (Table 14.2). Forty-four bird, 4 mammal, and 15 reptile species or subspecies

are restricted to mangroves. Endemic species are from a wide variety of vertebrate lineages: turtles, lizards, snakes, hummingbirds, egrets, rails, kingfishers, hawks, woodpeckers, passerines, bats, monkeys, sloths, and rodents (Luther and Greenberg, 2009). The number of endemic taxa associated with mangrove swamps has not been tabulated on a worldwide basis, and the number of mangrove specialized subspecies (as opposed to full species) is particularly

poorly known. Stotz et al. (1996) reported that only 87 species of Neotropical birds are found regularly in mangroves and for only 17% of these is mangrove a primary habitat. Of these, only four species are classified as being restricted to mangroves. Similarly, over 100 species of birds are characteristic of mangroves in south Asia and of these, approximately 30 are largely restricted to mangroves (King et al., 1975; Rasmussen and Anderton, 2005), with an additional 25 or so mangrove specialists in Australia (Simpson and Day, 1996). The low tree diversity, lack of terrestrial strata, and salinity of the environment probably combine to limit the number of successfully colonizing species.

14.1.4 The Role of Estuaries in Macroevolutionary Shifts

Because estuaries present a gradient of environmental conditions, are protected from the physical forces of the outer coasts, and are often highly productive, it is logical that they would present a habitat that is important for major evolutionary shifts within lineages from terrestrial and riverine ecosystems to open ocean and vice versa (Dunson and Travis, 1994). Examples of this include the incremental evolution of salt tolerance associated with the occupancy of estuaries in turtle and snake lineages. On a macroevolutionary scale, it is assumed that the ancestors of modern whales were primitive, carnivorous artiodactyls (*Archiocetes*) that occupied estuarine habitats approximately 50 million years ago. In these and other instances, estuaries are the cradles for the birth of important evolutionary innovations.

14.2 SEASONAL USE

14.2.1 Reproduction

In general, food resources far outstrip the habitat available for reproduction for most wildlife species associated with estuaries. The diversity and abundance of breeding birds, in particular, can be surprisingly low considering the concentrations found in estuaries at other times. Only about 50 of the 165 species of North American estuarine birds nest in or adjacent to estuaries, with the rest breeding in areas often quite distant. Similarly, Lefebvre and Poulin (2000) reported that of the 40–80 species that regularly inhabit the neotropical mangrove swamps they surveyed, only 3–15 species breed. A number of shorebirds, waders, and waterfowl species are joined by songbirds and small mammals to reproduce in marshes and mangroves at the estuarine

fringes. Sandbars and salt marsh islands provide a safe haven for colonial waterbirds, turtles, and at least one marine mammal (harbor seal *Phoca vitulina*). The calm open waters of large estuaries are sought after by a few species of ceteceans, such as the beluga (*Delphinapterus leucas*) and gray whales (*Eschrichtius robustus*).

14.2.2 Nonbreeding Use of Estuaries

A very high proportion of both the species and abundance of estuarine birds are found only during the nonbreeding season. In fact, estuaries support some of the most spectacular bird migrations with large portions of the continental populations of certain species concentrating in a single estuary during stopovers (Fig. 14.2). For example, over half of the 3–4 million Pacific Coast western sandpipers pass through the Copper River Delta in southern Alaska, a site that supports the highest concentrations of shorebirds for the flyway along the west coast of North America (Bishop et al., 2000). The two largest North American estuaries, San Francisco and Chesapeake Bays, support over two million waterfowl during the winter months (Perry and Deller, 1995; Takekawa et al., 2006). The concentrating effect of estuaries is not just found in birds. Some estuaries, such as the mouth of the St Lawrence River in Canada, support large concentrations of foraging marine mammals at certain times of the year.

14.3 SPECIALIZED ADAPTATION TO ESTUARINE LIFE

14.3.1 Tidal Cycles and Storm Surges

Regular tidal cycles cause profound habitat change from one to two times a day for estuarine wildlife. The most obvious effects occur in the intertidal zone where areas are regularly exposed or inundated with water. For example, exposed tidal mudflats provide a temporally available habitat for foraging shorebirds. At high tide, foraging birds can abandon inundated areas to forage in less affected habitats, in the way that sanderlings (*Calidris alba*), a small beach-adapted sandpiper, move between mudflats and outer coastal beaches during high tide (Connors et al., 1981). Tidal flows have a profound influence on the foraging of birds in deeper water as well. Double-crested cormorants (*Phalacrocorax auritus*) in the Columbia River Estuary of Oregon prefer to forage during ebb tides, because benthic fish are more exposed and

FIGURE 14.2 Migratory shorebirds, such as these red knots (*Calidris canutis*) and ruddy turnstones (*Arenaria interpres*), concentrate in temperate zone estuaries in the late spring to amass large volume of fat stores before heading off to the Arctic. In Delaware Bay, they feed voraciously on the eggs of horsehoe crabs (*Limulus polyphemus*), a highly threatened resource. Red knots breed circumpolarly in the high Arctic and migrate as far as South American, Australia, and South Africa. They concentrate along tidal mudflats in productive estuaries where they can accumulate up to 5 g per day and often make long nonstop flights (as far as 6000 km!) between their stopover sites (Piersma 2005).

phytoplankton (and its associated fish) is most abundant in areas of high tidal flow (Anderson et al., 2004).

Less predictable flooding can occur when normal daily tidal flow, rain, and wind align to bring water into areas that are normally spared regular tidal inundations. The reproductive effort of entire colonies of gulls, terns, and other colonial species can be wiped out by a flooding event (Fig. 14.3). Tidal marsh birds and mammals regularly elevate their nests compared to their nontidal marsh relatives. In certain songbirds, such as the salt marsh sharp-tailed sparrow (*Ammodramus caudicutus*) (Shriver, 2002), nesting resumes rapidly after loss from flooding, which allows a nesting cycle to occur during the 29.5 days

between the two high summer tides that characterize New England marshes (Shriver, 2002).

14.3.2 Salinity Gradients

Sea water, with its high salt content, presents a potential physiological challenge to animals dependent on consuming fresh water plants and animals that concentrate salt in their tissues. Adaptation to the saline environment is accomplished either behaviorally through selective use of water and prey items with lower salinity or physiologically through the concentration of saline solution in the kidney or in specialized glands (Table 14.3; Fig. 14.4). The need to reduce water loss appears to drive many of the adaptations for estuarine life, similar to those of animals in highly arid environments (Goldstein, 2006).

FIGURE 14.3 Laughing gulls (*Larus atricapillus*) along with other colonial water birds breed on isolated sandbars or islands to reduce predation on nests. These species often minimize the effect of flooding by building on floatable mats of detritus, using visible clues of high water for nest placement, having eggs that are resistant to submergence in salt water, rapid nest repair, and the ability to gather young that have floated away. Furthermore, colonial waterbirds may be able to renest rapidly and move colonies after flood events (Bongiorno, 1970; Burger and Shisler, 1980; Reinert, 2006).

TABLE 14.3 Adaptations to salinity in estuarine wildlife with examples

Adaptation	Example	Species	Reference
Dietary selectivity	Forage on plants with lower salt content	Meadow vole (*Microtus pennsylvanica*)	Getz (1966)
	Feed young prey with lower salt content	White ibis (*Eudocimus albus*)	Bildstein (1993)
Drink alternative sources of water	Dew	Meadow vole	Getz (1966)
	Rain water at estuary surface	Diamondback terrapin	
Reduce intake of brackish water and reduce loss of body water	Reduce drinking estuary water	Salt marsh snakes, turtles, marine mammals	Dunson and Travis (1994), Ortiz (2001)
	Reduce permeability of skin and water loss through mouth and nostrils	Salt marsh snakes and turtles	Dunson and Travis (1994)
Form concentrated saline solutions and expel salt from body.	Ability of kidney to concentrate salt in urine	Most mammals including marine mammals and a few salt marsh songbirds concentrate to 1000 mosM; Sea otters concentrate at much higher levels	Ortiz (2001), Goldstein (2006)
	Specialized salt glands	Expelled from mouth cavity of sea snakes and crocodiles; nares of birds; tear ducts of sea turtles	Schmidt-Nielsen et al. (1958), Dunson and Travis (1994), Heatwole (1999)
Reduced evaporative water loss through alternative means of heat dissipation and internal recycling	Bills and legs used to convect ''dry'' heat	Salt marsh sparrows	Greenberg et al. 2012
	Increased size of respiratory turbinates - structures that recycle expired water vapor	Marine mammals	Van Valkenburgh et al 2011

FIGURE 14.4 Salinity of food and water is a challenge for terrestrial species adapting to estuarine conditions. Most species use a combination of behavioral and physiological traits to reduce the osmotic stress. Small mammals are assumed to select less saline plant tissues and rely on the ability of their kidneys to conserve water and concentrate salt in urine. All mammals show abilities to concentrate salts in urine and the red-bellied harvest mouse (*Reithrodontomys flaviventris*) shown here has been demonstrated to be more salt tolerant than non-salt marsh species of harvest mouse (Fisler, 1963).

14.3.3 Coloration

A variety of salt marsh sparrows, shrews, voles, waterfowl, rails, and snakes show grayish and black (eumelanins) coloration rather than the buff, ochre, and rust (phaeomelanins) coloration of their nontidal relatives (Grinnell, 1913). This grayer and blacker coloration may improve background matching to the acid sulfate soils often associated with tidal marsh. Many estuarine reptiles and amphibians are darker or blacker overall and display brighter markers of carotinoid-based pigments, such as yellow and red (Neill, 1958). These color patterns may relate to living in darker and more turbid waters with the overall dark background color making the animal more cryptic and the brighter markings allowing signal detection at a longer distance.

14.3.4 Turbidity

The often highly turbid water of estuarine shallows is an adaptive challenge to many animals. One adaptive solution is a shift away from visual to other sensory modes, particularly tactile foraging. Such a shift in visual ability between surface and submerged foraging has been described for the American crocodile (Fleishman et al., 1988). A number of birds sift or plough (see below) with their bills to increase the area ''searched'' tactilely in shallow water or soft substrates.

14.3.5 Social Organization

The juxtaposition of productive habitats for feeding (open water, mud flats, tidally inundated marshlands) with relatively small areas available for reproduction has favored the development of aggregated patterns of spatial use. Nesting colonies of gulls, terns, and large wading birds are placed on small islands, which are relatively free from potential predators (Fig. 14.3). During the non-breeding season, most estuarine birds and marine mammals are found in aggregations or flocks. Many of the foraging resources, benthic invertebrates, submerged aquatic vegetation, and fish, are patchily distributed in a way that is not economically defendable, forcing numerous animals to recruit to rich foraging sites (Kushlan, 1981). In addition, owing to fluctuations in tidal conditions, food concentration varies in time and space.

The presence of birds in flocks and mammals in pods reduces the threat of their being depredated and improves foraging efficiency. Estuaries are often very open and provide little cover. In terms of predation, animals in groups are often less vulnerable to predator attacks because the predator is more likely to be detected (more eyes) and it is more difficult to capture an individual that is in a tightly organized group. Shorebirds are more likely to be successfully attacked by a falcon when alone or in a small group than in a larger flock (Page and Whitacre, 1975).

Foraging efficiency can be increased through the use of other animals as sources of information. One elegant demonstration of this so-called ''information hypothesis'' is made by species-specific models of egrets and herons on a mudflat in a Panamanian estuary (Caldwell, 1981). Several species of heron are attracted to the snowy egret (*Egretta thula*) foraging model over all of the others. The snowy egret is the most efficient species at locating schools of fish, and all herons that join them increase their foraging rates. Snowy egrets are able to displace the other

FIGURE 14.5 Social foraging is important for estuarine animals. Most often the benefits of group living relate to the reduction of predation, but in some cases, such as for bottlenose dolphins (*Tursiops truncatus*), driving fish onto a muddy bank along the southeast coast of the United States (Shane et al., 1986), the successful hunting of mobile group-living prey, such as schools of fish, benefits from cooperation.

herons from the best patches; therefore, by gaining information on good foraging conditions from their subordinates, snowy egrets also benefit from the association.

A number of small cetaceans, pinnipeds, and diving birds hunt fish cooperatively, thus getting a strong direct benefit from group life (Fig. 14.5). For example, large flocks of cormorants form long densely packed lines at right angles to their forward movement (Bartholomew, 1942). This line moves schools of fish in front of them and allows individuals to capture fish from the school without the fish scattering. These large flocks are joined by gulls that hunt the concentrated fish from above.

14.4 FACTORS LIMITING AND REGULATING WILDLIFE POPULATIONS

14.4.1 Density-Dependent Processes

Populations have the potential for exponential increase, but are universally limited from realizing this indefinitely. Populations can be limited by external factors that operate independent of density and provide a fixed limit or simply a periodic reduction in the population. True regulation occurs when fecundity or survival declines in a predictable

manner with increasing density as an environmental carrying capacity is reached. Density-dependent regulation can play out over the annual cycle and sometimes over large areas. Since most estuarine bird populations are migratory and could experience limitation or density-dependent regulation at different seasons and sites, it is not surprising that few studies of estuarine species have developed an overall picture of the factors that limit or regulate a bird population that uses estuaries only seasonally.

Black-tailed godwits (*Limosa limosa*) wintering in Great Britain have increased over a period of years; populations in estuaries with high food supply remained stable and populations in resource-poor estuaries increased. Once settled in the satellite estuaries, godwits were less likely to survive the winter than in the core-stable estuaries. This suggests that many godwits are forced to occupy suboptimal wintering sites when the overall density increases. This colonization of suboptimal habitat during population increase is referred to as the *buffer effect* (Gill et al., 2001). Studies on godwit breeding grounds in Iceland (Gunnarsson et al., 2005b) have demonstrated that these growing populations expanded into suboptimal birch bogs rather than superior and more stable marsh habitats. Thus, this estuarine species experiences a buffering effect at both ends of its migration. Furthermore, population tracking using stable isotope signatures of feathers molted on the breeding grounds (Gunnarsson et al., 2005a) has established

that the birds that winter in buffer habitats were likely the same as those that colonized the buffer habitat during the breeding season.

For most estuarine species, we do not have such comprehensive population data to address the role of estuaries in long-term population trends. However, we can examine features of the behavior of populations that indicate if competition for resources might be occurring.

14.4.2 Competition

Competition occurs when individuals have a negative impact on the ability of other individuals to garner resources necessary for survival or reproduction. Competition can be based purely on the ability of one individual to reduce the abundance of resources available to others or can occur when the presence of individuals interferes with the access to the resource. A territorial animal invests its energy into obtaining access to space and then defends it against the access of other individuals. Territorial systems are common among estuarine birds, but vary considerably in their stability and the nature of the resource in the space being defended. Some animals, including many songbirds in salt marshes and mangrove forests, maintain ''all-purpose'' territories, where all of the needs of an individual, pair, or family group are met. Other animals maintain territories only for specific purposes. In areas where nesting habitat is much smaller than foraging habitat, birds defend nesting small territories and feed in larger shared feeding areas. This appears to be the pattern among certain salt marsh sparrows (Johnston, 1956; Post and Greenlaw, 1994) that nest in densely clustered territories within relatively flood-free marsh regions. These forms of nesting territories may be as tiny as the length of an outstretched bird bill, but are definable among colonially nesting birds, such as gulls and terns.

Most birds associated with mudflat or aquatic habitats in estuaries show clumped distributions around good feeding areas, but within these aggregations, it is sometimes possible to find individuals (e.g., Tripp and Collazo, 1997) defending feeding territories. In this case, the benefits of territoriality can be measured in terms of the increase in feeding efficiency realized when competitive conspecifics are eliminated or reduced in numbers. The cost of defense can be quite high, and birds lose some of the antipredatory advantages of group life. So the presence of feeding territory suggests that food is abundant enough to defend and scarce enough so that it pays to chase off other birds.

Despite the importance of aggregations and flocking, these groups are not without their competitive

tensions (Kushlan, 1981). For shorebirds, access to the best foraging sites is often controlled by dominant individuals that force subordinates to other areas (Goss-Custard, 1980). This effect may be density dependent and hence regulates local population abundance and the impact of that population on its prey. Dominance is often associated with age or sex, which leads to segregation of habitat. For example, in bar-tailed godwits (*Limosa lapponica*) wintering in subtropical areas of Australia, males are found primarily in superior seagrass bed habitat, whereas females are more broadly distributed on sandy shores and seagrass beds (Zharikov and Skilleter, 2002). Among highly migratory species, spatial segregation often plays out over very large areas, resulting in distinct latitudinal separation of males and females, yearling and older birds (Mathot et al., 2007).

14.4.3 Predation

The effect of predators on estuarine wildlife populations can be seen in studies of the effect of raptors on shorebirds. Through the systematic observation of diurnal predators and examination of pellets and remains at favorite perches, Page and Whitacre (1975) estimated that falcons, hawks, and owls were removed from 8 to 21% of the individuals of different shorebird species in a California coastal lagoon. However, how mortality due to predation varied with density was not investigated in this study. As discussed in Section 14.4.1, only density-dependent sources of mortality tend to contribute to population regulation. In a more recent study, it was shown that the per capita loss to Eurasian sparrow hawks (*Accipiter nisus*) occurred at sites with higher density of dunlins (*Calidris alpinus*) (Whitfield, 2003), suggesting a regulatory role for predation in this wintering shorebird population. In addition to the local density, both behavior of the birds and the physical environment have been shown to play a role in levels of predation. The tidal cycle has been shown to play a large role in the success of falcons hunting shorebirds, with the greatest success occurring immediately after peak high tides—when birds are concentrated near the shore (Dekker and Ydenberg, 2004).

14.4.4 Disease

The incidence of disease and parasites increases with population density for two reasons: (i) the decline in conditions and increase in the stress level make animals more susceptible to infection and (ii) transmission is facilitated by reduced individual distances. Disease and parasites tend to be endemic in populations, causing low to moderate levels of mortality.

Under these conditions, the role of these factors in population regulation is poorly understood. Instead, most attention is focused on epidemic diseases (epizootic) that spread rapidly and cause very high levels of mortality in a short period of time. The tendency of birds and other animals to aggregate in estuaries probably facilitates rapid disease transmission. The best-known examples of such disease transmission estuarine habitats are reported from birds, and perhaps the best studied of these is avian cholera (Friend, 1992). In addition to the chronic diseases that have been known to affect birds for a long time, ornithologists have become increasingly aware of emerging diseases that may be novel in estuarine bird populations. The best-known example is the outbreak of H5N1 strain of bird flu in poultry and wild geese in Asia; its virulence and rapid spread has focused the attention of ornithologists and human health scientists alike on avian influenza. This is a novel strain with unknown and changing properties. However, avian influenza was first documented in the early 1960s (Alexander, 2000), and is likely to have had a long history in bird populations. Most strains show low levels of pathogenesis and low frequency of isolates in most wild bird populations studied. What is new is the highly virulent strain. Estuaries may play an important role in the spreading of any avian influenza because Anseriformes, particularly geese and dabbling ducks (Olsen et al., 2006), and Charadriiformes (gulls, terns, and wading birds) are found in high frequency in these. West Nile Virus is another example of an emerging avian disease, although it has not been shown to be especially prevalent in estuarine bird populations. The outbreaks of traditional diseases and the advent of new strains of avian disease taken together with the often high densities of birds found in the remnant wetlands makes it critical to increase research in the field of occurrence and spread of pathogens in estuarine environments.

14.5 ECOLOGICAL ROLE OF WILDLIFE

14.5.1 Herbivory

Terrestrial herbivores. Microtine rodents are probably the most abundant vertebrate herbivores in estuarine marsh systems. Voles in the genus *Microtus* are locally common in marshes along both coasts of North America. Voles feed primarily on grass stems along well-defined runways in high marsh. The creation of runways, which facilitates the movement of voles through the thick, grassy marsh vegetation, requires that voles harvest the entire above-ground portion of the plant, which can begin a process of local erosion. Large herbivores are notably missing from most estuaries, although browsers, such as deer and elk, can be found at the upper edges of some marsh systems. In some regions, deer can also be important in low marshes. sika deer (*Cervus nippon*), native to Asia but introduced in Europe and the United States, have been shown to greatly reduce the vegetative cover and increase open areas in *Spartina* marshes in England (Hannaford et al., 2006), which can result in an increase in plant diversity at moderate levels of grazing and a decrease in diversity at high levels of grazing. A subspecies of the white-tailed deer (*Odocoileus virginianus mcilhennyi*) is assumed to have specialized on salt marshes along the Gulf Coast although the population may have suffered a large amount of genetic introgression from the inland white-tailed deer in recent decades. Large grazing animals were probably more common in estuaries until the most recent glaciation when large megafaunal herbivores were eradicated from regions with relatively large expanses of tidal marsh (Levin et al., 2002).

What we know about the potential impact of large grazers on salt marshes is derived from studies of livestock or feral livestock animals (Bos et al., 2002) (Fig. 14.6). Predictably, the most immediate effect of livestock herbivory is to reduce the standing crop of favored forage plants leading to the spread of less palatable species and weakened zonal patterns of vegetation (Shanholtzer, 1974).

Aquatic herbivores. Seagrass beds, dominated by eelgrass (*Zostera* sp.) in temperate regions and turtle grass (*Thalassia*) in the tropics and subtropics, cover the shallow substrate of estuaries throughout the world. Herbivory is generally low on these plants compared with other aquatic plants, perhaps due to the high content of structural carbohydrates (cell wall material) and minerals, as well as the presence of tannins, flavonoids, and other secondary compounds (Thayer et al., 1984). Their use by wildlife is restricted to a few species: green turtles (*Chelonia mydas*; Fig. 14.7) and species of manatees and dugongs in the tropics, and ducks, coots, geese, and swans in temperate regions (Thayer et al., 1984; Bortolus et al., 1998). The birds and turtles function as grazers, cropping the palatable portions of the plants. In contrast, herds of dugong plough trails through seagrass beds, digging up the plants from the rhizomes and causing more extensive, longer-term disturbances.

In the temperate zone, a number of waterfowl species graze on seagrass beds, particularly eelgrass
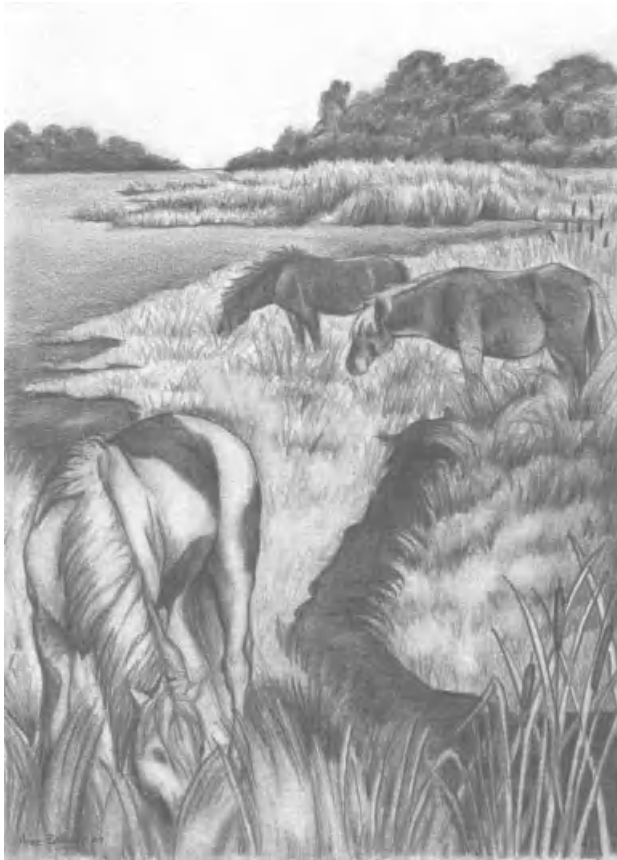
FIGURE 14.6 Feral populations of introduced horses (*Equus caballus*, Furbish and Albano, 1994; Levin et al., 2002) in marshes in southeastern United States feed heavily on cord-grass (*Spartina alterniflora*) and can have a locally important effect on marsh structure and nutrient cycling.

FIGURE 14.7 The effect of green turtle (*Chelonia mydas)* herbivory on Caribbean turtle grass beds has been particularly well studied. Seagrass comprises close to 90% of the diet of green turtles, the only reptile that grazes significantly on seagrass. They overcome the low availability of accessible nitrogen and other nutrients by cropping close to the base of the plant and through their behavior of grazing plots of seagrass on a regular cycle, thus maintaining plants at an early stage of regrowth.

and widgeon grass. The most specialized of these is the brant (*Branta bernicla*), which concentrates most of its fall and winter feeding on these species (Cottam et al., 1944). The loss of seagrass beds along the Atlantic coast of North America and Europe to wasting disease has caused rapid and marked declines in brant populations, from which there has been only a partial recovery. Some waterfowl species, such as redheads (*Aytha americana*), have shown local declines where seagrass beds have retracted, and others, such as the canvasback (*Aythya valisineria*) have shown a dietary shift to invertebrates. The loss of submerged aquatic vegetation due to reduced water quality in the Chesapeake Bay has led to very large population declines in some species or almost complete abandonment of the bay by others. Population increases in this region are restricted to grazing geese and swans that graze upland habitats (Perry and Deller, 1995), although there has been evidence of recovery for other species in recent years.

The role of herbivory in these systems has undoubtedly changed over historic times as the populations of large vertebrate herbivores have declined, usually due to human exploitation (Jackson et al., 2001). For example, in the Caribbean, green turtle populations are estimated to have declined 15- to 30-fold in the Caribbean in the past 300 years and dugong populations may be as much as 200 times smaller than those a century ago. Although the declines may not be as dramatic, waterfowl populations have decreased in temperate estuaries as well.

Ecological engineers. Ecological engineers are species, usually herbivores, whose activities drastically change the basic structure and hydrology of a habitat. Two examples of ecological engineers in estuaries are the muskrat (*Ondontra zibethicus*) and the snow goose (*Chen caerulescens*). Common in fresh or brackish tidal marshes, muskrats reduce the cover
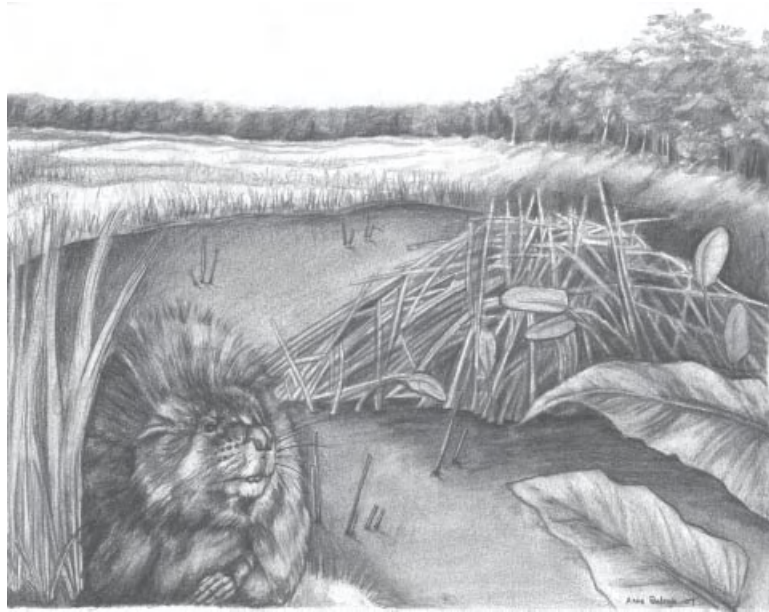
FIGURE 14.8 Muskrat (*Ondontra zibethicus*) and den with moat around it. The herbivory and construction activity of muskrats greatly changes the topography and hydrology of estuarine marshes and earns it the designation ''ecological engineer''.

by dominant vegetation types through herbivory, den construction, and channel formation, which creates open water and causes the local topography to be hummocky in nature (Fig. 14.8, Errington, 1961). Snow goose flocks locally denude areas in salt marsh by pulling plants out by the rhizomes, which inhibits regrowth. Long-term effects can include depletion of soil nutrients and erosion, and reduction of invertebrate diversity and abundance (Sherfy and Kirkpatrick, 2003). Usually the effect is local and may serve to create some habitat heterogeneity. With rapidly increasing goose populations, the damage has been more extensive in some areas.

14.5.2 Pollination and Seed Dispersal

Tidal marshes tend to be dominated by a few species of grasses. With the exception of some emergent shrubs and vines at the upper edge of marshes, few estuarine plants produce fleshy fruit to attract animal dispersers. Salt marsh grasses tend to produce relatively small seed crops and seed banks are poorly developed (Leck, 1989), thus attracting few seed dispersers, so the seeds that are produced are transported primarily by water through tidal movement. A number of sparrows and small mammals forage seasonally on spartina or rush seeds and, in Australia, the rare parrots of the genus *Neophema* winter in salt marshes feeding on the seeds of Chenopods (Loyn et al., 1986). Although primarily detrimental to the seed crop, the activities of these granivores may dislodge and free

uneaten seeds into the water for further dispersal. For example, Shanholtzer (1974) observed that in areas grazed by livestock concentrations of seeds could be found in the water resulting from the activity of the grazers.

Animals may also be responsible for longer distance dispersal along migration routes. Small numbers of viable seeds can be found on the feet, feathers, and fur of animals (Vivian-Smith et al., 1994). Even this small number of seeds transported by migratory birds provides an opportunity for long-distance dispersal that is not offered by water transport and may account for some large disjunct distribution patterns. In contrast to temperate salt marshes, mangrove forests are inhabited by both frugivorous (seed dispersing) and nectarivorous (pollinating) species. In particular, there appear to be a few hummingbirds or sunbirds that specialize on this habitat and feed commonly from the flowers of certain mangrove species.

14.5.3 Top–Down Control of Invertebrate Populations

Within estuaries, the greatest focus has been on shorebird predation on benthic invertebrates, partly because the concentration of individuals and species in a relatively simple habitat is such a striking phenomenon. Caged exclosure studies have established that shorebird predation can have a large effect on their invertebrate prey base (Schneider, 1978; Schneider and Harrington, 1981; Quammen, 1984;

Wilson, 1991). The magnitude of the effect varies directly with the density of birds and life history characteristics of the prey, and indirectly with the particular habitat. For example, Quammen (1984) found that shorebirds in southern California estuaries depleted prey (polychaete and oligochaete worms) substantially in areas of muddy, but not sandy substrates. Mercier and McNeil (1994) detected a significant decline in polychaete worms by shorebird predation in a Neotropical estuarine lagoon only during fall migration. Some studies (Schneider, 1978; Botto et al., 1998) demonstrate that shorebirds differentially reduce the most common species. However, shorebird predation is not currently assumed to have a strong effect on infaunal diversity. Shorebirds are often size selective, preferring larger size classes of certain prey types and differentially preying upon the reproductive size classes. Because of this, they may have a long-term influence on population productivity. Shifting our focus to deeper water, diving ducks can also harvest a substantial (40–90%) portion of the shellfish from benthic beds (Hamilton, 2000). The take-home lesson for those carrying out studies of the impact of shorebirds and ducks is that the affect of birds is highly variable, but under some circumstances it is surprisingly large.

14.6 FORCES OF CHANGE

14.6.1 Sea Level Rise and Climate Change

Sea level rise transforms tidal flat to estuary, low marsh to tidal flat, and high marsh to low marsh. Depending on the shape of the estuary and the nature of land use at the upper edge of the marsh, sea level rise has resulted in a variable but significant reduction in the number of coastal wetlands—with estimates of loss ranging from 0.5–1.5% per year for North America (Titus, 1988; Church et al., 2001). Sea level rise may bring increased salt water intrusion and increases in salinity (Titus, 1988), which may affect species adapted to brackish conditions. Changes in salinity have occurred historically as well owing to a decrease in freshwater flow into the estuary.

In addition to sea level rise, changes in climate could lead to more frequent and/or intense storms and is likely to result in increased erosion, flooding of low lying areas, intrusion of salt water, wetland destruction, and negative impacts on the biology and ecology of tidal marsh endemics. On the basis of the analysis of current habitat use and response to periodic flooding events, some specific predictions have been made about the short- and long-term effects of

sea level rise on vertebrate populations (Daniels et al., 1993; Erwin et al., 2006). For many species, increases in shallow water and tidal flat habitats may create foraging opportunities. However, species of colonial waterbirds that concentrate their breeding efforts on salt marsh islands may lose their traditional nesting sites. Species dependent on low marsh habitats, such as seaside sparrows, may see their habitat fragmented as much of it is flooded or transformed into tidal flats (Shriver and Gibbs, 2004), and others that depend on high marsh may see loss of habitat as well, particularly if human development prevents marsh migration. In Great Britain, the twite (*Carduelis flavirostris*), a small seed-eating finch, is dependent on the seeds of salt marsh plants in the winter, particularly in the lower marsh zone (Atkinson et al., 2004). A sharp decline in twites has been tied to the loss of low marsh. Species that nest on sand bars and marshes in estuaries occur in a narrow optimum habitat that minimizes the threats of flooding and predation. An increase in flood incidence may push them to nest in areas where predation levels are too high to sustain their populations.

Climate change may also have indirect effects on estuarine fauna, particularly for migratory animals that inhabit different ecosystems during other periods of their life cycle. For example, one of the predicted effects of climate change is the drying of wetlands in the prairie potholes, sometimes referred to as the ''duck factory'' of North America. This would reduce the density and reproductive output for ducks in this region (Sorenson et al., 1998), which would lead to fewer birds migrating to estuaries.

14.6.2 Invasive Species

Estuarine tidal marshes are susceptible to shifts in dominant species of vegetation that come with the spread of invasive species. Low salt marsh and adjacent unvegetated mudflats along the coasts of Tasmania, New Zealand, northern Europe, and continents bordering the eastern and western Pacific Ocean are being invaded by *Spartina* species, mostly *Spartina alterniflora*, which often hybridizes with the local native species. At the upper edge of marshes along the Atlantic Coast of North America, a strain of the common reed (*Phragmites australis*) is spreading into areas once dominated by *Juncus, Spartina*, and *Iva* shrubs. The effect of such invasions on estuarine vertebrates is poorly documented, but recent research has shown that the invasion of *Phragmites* favors certain generalist bird species over tidal marsh specialists (Benoit and Askins, 1999). At low densities, *Phragmites* creates habitat heterogeneity within the native marsh vegetation, but when it spreads to form large, single-species

stands, resources for some marsh nesting species disappear. The invasive *Spartina* and *Phragmites* support local increases in marsh wren populations, which may further impact endemic sparrows. Recent research in San Francisco Bay suggests that *Spartina* growing on formerly unvegetated mudflats may serve as a death trap, attracting low nesting sparrows and rails to attempt breeding in areas that are prone to flooding (Guntenspergen and Nordby, 2006). Mudflat invasion by *S. alterniflora* is also expected to reduce high-quality shorebird habitat in the coming decades. Recent work in China, where *Spartina* is replacing native *Phragmites* marsh, has documented higher bird diversity in the native vegetation, reversing the phenomenon from eastern North America (Gan et al., 2009).

Estuarine invertebrate assemblages, the prey base for so much estuarine wildlife, are also prone to local invasions, many of which are initiated by animals transported on ships. Although invasive species now comprise up to 90% of the benthic invertebrates in some estuaries (Cohen and Carlton, 1995), the impact of this faunal shift on vertebrate populations is poorly known. Some species, such as one species of isopod in San Francisco Bay, cause increased erosion of tidal marsh areas. Lesser scaup (*Aythya affinis*) in San Francisco Bay switched from feeding on native *Macoma balthica* to now locally dominant *Potamocorbula amurensis* clams, and were able to extract food at a higher rate because the introduced species tended to be smaller and burrowed more shallowly in the sediments (Richman and Lovvorn, 2004). A more long-term impact may be realized as the invasive species concentrates greater quantities of contaminants than the native one.

Wildlife species are frequently introduced from one region to another, and some quickly colonize tidal marshes. The most globally transported taxa are Norway and black rats (*Rattus norvegicus* and *Rattus rattus*) and house mice (*Mus musculus*). Rats and opossums, in particular, may become important nest predators where they are introduced. The possibility of their transporting novel strains of diseases to coastal areas has not been explored.

14.6.3 Fire

Marsh vegetation at the fringes of estuaries is subject to naturally ignited fires at varying degrees of frequency depending on climate and weather patterns. In North America, for example, the natural fire frequency is very low in west coast marshes, somewhat higher in marshes of the northeast and mid-Atlantic regions, and highest in Florida and along the Gulf Coast. In some regions, fire is used as a tool for the management of wildlife populations. The general theory is that fire favors the growth of vegetation that is preferred forage of target species such as geese and other waterfowl populations. Fire releases nutrients bound in standing vegetation, and causes a pulse in primary productivity. Fire has traditionally been used by trappers to augment resources for muskrats and to make marshes more accessible. In South America, fire is commonly used to enhance marsh habitat for livestock. Unfortunately, in the short run, the removal of vegetation probably makes nesting birds and small mammals more vulnerable to predation. In one of the few community-level studies, researchers in Argentina found that marsh burning favors the colonization by a variety of generalist pampas grassland species over the two spartina marsh specialists (Isacch et al., 2004).

14.6.4 Pollution

One of the largest human impacts on estuaries is the increase in nutrients from upstream agricultural and other runoff and the indirect effects this has on the food resources on which wildlife species depend. The role this may play in the depletion of submerged aquatic vegetation and the subsequent decline in estuarine waterfowl is discussed above. Such pollution can also cause declines in shellfish beds, which support large numbers of diving ducks. Nutrient loading, together with increased water temperature, has resulted in an increase in harmful algae blooms (HAB) including red and brown tides caused by dinoflagellates (Landsburg, 2002). At high densities, these algae produce substantial amount of neurotoxins, which can cause illness or death in wildlife species that consume fish that have fed on the affected algae or phytoplankton. In past decades, high mortality linked to HABs has been reported for a variety of species, including a number of birds, whales, and manatees.

Human-introduced chemical contaminants bind to sediments in estuaries and some, including methyl mercury, selenium, passive diffussion bags (PDBs), and trace metals, bioaccumulate up the estuarine food chain (Takekawa et al., 2006). Phorbol 12,13-dibutyrate (PCB) contamination in coastal Georgia marshes was found to be associated with a high frequency of strand breakage in the DNA of clapper rails (Novak et al., 2006; Fig. 14.9). This level of contamination has ramifications on human health because the rails are game species commonly hunted and consumed by local residents. Mercury contamination, for which atmospheric fallout is the primary source, can be a particularly severe problem (Takekawa et al., 2006), causing acute toxicity in fish, birds, and

FIGURE 14.9 Estuarine ecosystems often suffer from the influx of contaminants such as heavy metals or pesticides that drain into the systems from urbanized and agricultural lands in the often very large watersheds. Many of these contaminants bioaccumulate, meaning that they are found in animals in increasing concentrations as one moves up trophic levels. Clapper rails (*Rallus longirostrus*) in Georgia have been shown to have high levels of PCBs, which lead to demonstrable chromosome damage (Novak et al., 2006).

mammals. High-level exposure damages the central nervous system, whereas low-level exposure affects reproduction in vertebrates (Wolfe et al., 1998). Broad-spectrum pesticides are often applied to tidal marshes for mosquito control. This practice may be exacerbated by the perception that the habitat is a source of vectors for emerging diseases, such as the West Nile Virus (Takekawa et al., 2006).

14.6.5 Salt Production and Shrimp Ponds

Salt marshes and mangroves have been impounded for salt production for hundreds of years in many estuaries throughout the world, particularly Europe, California, and China. These evaporation ponds replace the natural vegetation and thus have a direct impact on estuarine wildlife. However, in many cases, blooms of brine shrimp provide feeding habitat

for a large number and high diversity of migratory shorebirds and waterfowl (Warnock et al., 2002) and could be managed to improve their value to these bird species.

Mangrove swamps have also been modified for shrimp fishing and low level shrimp aquaculture for a long time. Since the early 1980s, however, large areas of mangroves, particularly in Asia and Western South America, have been impounded for intensive shrimp farming and other forms of aquaculture. Fish and crab aquaculture has expanded enormously in the past few decades along China's estuarine shores at the expense of natural mangrove swamp and marshland. The impact of this conversion on wildlife has not been directly assessed, but it is likely that, although the ponds themselves are used by foraging wading birds, the bulk of wildlife diversity is eliminated.

14.6.6 Direct Interactions of Humans and Wildlife

Estuaries have been important locations for human settlement since their most recent reformation 5000–9000 years ago during the early Holocene. Estuaries provided a diversity of resources to preagricultural ''hunter–gatherer'' societies and were often the centers of early settlement on coastlines throughout the world (Ames, 1999; Ercolano and Carballo, 2005). Abundant shellfish, fish, mammals, and birds, in particular, provided a rich, localized food source that allowed for the development of more sedentary settlements.

Modern hunting. Subsistence and recreational hunting has been conducted in estuarine habitat for millennia, but it is unclear what impact such activities had on wildlife populations. However, in the eighteenth and nineteenth centuries, hunting shifted, at least in North America, toward market hunting. In particular, the invention and increased use of shotguns and other guns that could deliver a large amount of munitions in a short period led to the widespread depredation of huge numbers of shorebirds and waterfowl (Hornaday, 1913). Many of these birds were sold for food, while others, including egrets and herons, were collected to provide plumes for decoration (e.g., women's hats) led to the widespread loss of wading birds.

By the end of the nineteenth century, large flocks of waterbirds present in the earliest days of European settlement were decimated and some formerly abundant species were hunted almost to extinction. During the early years of the twentieth century, migratory birds received either complete protection (including most shorebirds) or the beginnings of scientifically based hunting regulation (most waterfowl). Other wildlife is

FIGURE 14.10 Diamondback terrapin (*Malaclemys terrapin*). In addition to being a staple food for coastal families, from the nineteenth century, terrapins were exported to exclusive restaurants as a delicacy. Overexploitation and habitat loss caused a large population crash in the early twentieth century and gradually terrapin meat fell out of favor. Terrapin populations recover slowly from declines and still suffer from habitat degradation and from loss due to being a by-catch for fisheries and crabbing operations. A few states in the United States allow large-scale exportation to Asian markets. Therefore, some populations remain threatened to this day.

hunted or trapped in estuaries throughout the world, including fur-bearing mammals, small cetaceans, turtles, and turtle eggs (Fig. 14.10).

Humans and wildlife have competed for the same food resources in estuaries since their reformation 7–10,000 years before present (ybp). However, only very recently have any studies been conducted to examine the impact of human fishing and gathering activities on resources that support local wildlife. Semipalmated sandpipers (*Calidris pusilla*) congregate in the Bay of Fundy to feed on abundant amphipod prey, but this sandpiper has declined dramatically because of a local industry of digging and collecting worms for fish bait from the bay's mudflats (Shepherd and Boates, 1999). Similar extractive activities are particularly common in Asian marshes. A further example can be found in the decline in horseshoe crab (*Limulus polyphemus*) eggs, as they are used as food by migratory shorebirds, the adults are captured and used as bait in the eel and whelk fisheries, and a product is also extracted from them for the pharmaceutical industry. Outside of birds, the degree of competition for declining populations of migratory salmon between sea lions and humans remains controversial.

Competition between humans and wildlife: A broad perspective. The competition between wildlife and humans for estuarine resources involves far more than interactions over specific food resources. Throughout the world, estuaries are prime locations for the growth of human cities. Urban and suburban development is responsible for the conversion of considerable wetlands and beachfront habitat that provide critical habitat for estuarine wildlife. Even in areas that have not directly been developed for human habitat or occupancy, associated development (airports, refuge disposal sites, and recreational areas) are often located along the shoreline of estuaries. Burton et al. (2002) demonstrated that, even where appropriate mudflat habitat was present, different species of shorebirds occurred in reduced abundance in the face of local urban development, the presence of roads and railroad lines, and even nearby footpaths. Shipping and recreational boating activities further reduce the areas of open water where wildlife can avoid direct human disturbance. Animals that need undisturbed sandspits for nesting or calfing are particularly vulnerable, and colonies and rookeries have been displaced to the few remaining protected shorelines. For example, in coastal Virginia, where most of the barrier islands are protected, more than 80% of the coastal-breeding gulls and terns were found on natural barrier island beaches (Erwin, 1980). However, in New Jersey, with only 25% protected beach front, almost all of the gulls and terns were forced to nest on dredging and in salt marsh where they suffered from competition from the dominant herring gulls (*Larus argentatus*). The effects of human presence can be at the level of the landscape. DeLuca et al. (2004) developed an ecological integrity index of for salt marsh birds based on the number and types of birds present. When comparing different marshes embedded in distinct landscapes, they found that the diversity of birds, particularly specialized marsh birds, was greatly reduced by relatively low levels of nearby urban/suburban development.

Few of the world's estuaries and none of the major estuaries are free from the pervasive effects of human

settlement. The restoration of modern estuaries to past conditions is impossible. However, even the most heavily impacted of estuaries support a surprising abundance and diversity of wildlife species. It is imperative that estuarine ecologists continue to study the responses of wildlife to anthropenic change to develop scientifically sound strategies for wildlife conservation. In this way, despite the competition for every resource that supports estuarine ecosystems, healthy populations of people and wildlife will be able to coexist in the distant future.

14.7 CONCLUSIONS

In the face of a dizzying array of details that come from ecological studies of wildlife in estuaries, it is useful to unfocus our gaze and try to summarize major ecological characteristics of estuarine wildlife. Here, in a few numbered bullets, are a few grand themes that have emerged from decades of research on estuarine systems:

1. The estuarine fauna, while showing moderate levels of species diversity, display an enormous range of functional diversity. The range of foraging-related morphological adaptations and body size is equaled in only a few ecosystems.

2. Although relatively low in endemic taxa, estuaries have probably played a key role in major macroevolutionary events that involve invasion of the marine environment from terrestrial, palustrine, or lacustrine habitats and vice versa.

3. Estuaries often support high levels of abundance of wildlife species locally and seasonally. However, the abundance we observe today is probably a small fraction of what could be found historically before human population density increased around estuaries and throughout their watersheds.

4. Migration and seasonal use characterize most wildlife species use of estuaries.

5. Coloniality or breeding systems that approach coloniality are particularly prevalent because rich feeding areas in estuaries are often spatially separated from breeding areas that are safe from flooding and predators.

6. Flocking and other forms of aggregated distributions are also characteristic of both aquatic and terrestrial species in estuaries.

7. Food resource use by wildlife species is focused on fish in the deeper embayments, fish and

shellfish in moderate to shallow waters, seagrass and other submerged aquatic vegetation in the shallowest waters, benthic invertebrates on mudflats, invertebrates, and terrestrial vegetation in the fringing marshes and mangroves. All of these have proven sensitive to changes in land use and chemical input in and around the estuaries.

8. Direct herbivory rates are often low, with much of the energy and biomass consumed by vertebrates through a detritivore food chain.

9. Vegetation is often simple in structure, dominated by a few species, and organized in a zonal pattern of distribution. Where the activity of animals, flooding, fire, and other modes of disturbance disrupt these areas of single species dominance, the diversity of animal species often increases, but at the expense of specialists. Some components of estuarine systems seem to be very prone to shifts in dominance from native to invasive species and the impact of this on wildlife is poorly known.

10. Estuaries have been the focus of human activity, probably for tens of thousands of years. Wildlife and humans have been and continue to be in direct competition for the abundant food resources found in estuarine waters. Human activities associated with development in the watershed of estuaries and the use of estuaries for shipping and other economic activities continue to threaten the wildlife populations and the estuarine resources they depend on.

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CHAPTER FIFTEEN

ECOSYSTEM METABOLISM

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15.1 INTRODUCTION

The metabolism of coastal ecosystems provides an integrated measure of the dynamic changes in ecological processes, including food web interactions among organisms and biogeochemical cycling of elements (Odum, 1967). Spatial and temporal variations in these processes, which are constrained and driven by environmental conditions, are thus reflected in the overall production and respiration of the ecosystem (Hopkinson and Vallino, 1995; Gazeau et al., 2005c). Associated with feeding, growth, and death of each organism are physiological processes that involve the formation and utilization of organic matter. *Anabolic* processes use external energy to synthesize new organic matter, and *catabolic* processes derive biochemical energy from decomposition of these organic molecules. Together, these physiological processes comprise the integrated metabolism of each organism. Coastal ecosystem metabolism can be measured as the summation of anabolic and catabolic rates of all organisms in the system (Kemp et al., 1997). Metabolic rates can be inferred from measurements of temporal trends and/or spatial gradients in key dissolved metabolites (e.g., oxygen (O_2), carbon dioxide, ammonium, nitrate, and phosphate) and from measurements of fluxes across ecosystem boundaries (Lee, 2001; Caffrey, 2004).

Coastal ecosystem metabolic rates provide a broad measure of the ecological condition of a system in terms of its overall rates of biogeochemical transformation and its interactions with adjacent ecosystems (Heath, 1995). The net production (i.e., production minus consumption) of organic matter in an ecosystem not only represents a measure of the system's balance and coupling between anabolic and catabolic processes but also reflects the import and export of biologically important substances. Organic matter production in a coastal ecosystem derives from light-driven photosynthesis of all plants, such as phytoplankton, benthic micro- and macroalgae, emergent wetland, and submersed vascular plants (seagrass), as well as from chemoautotrophic production (e.g., nitrification, sulfide oxidation) driven by the chemical energy of reduced ions. Metabolic consumption of organic matter in a coastal ecosystem is the sum of its respiratory processes, which come in a variety of forms including (i) aerobic respiration (characteristic of most higher organisms and some microbes), a process in which O_2 is the terminal electron acceptor; (ii) anaerobic respiration (characteristic of many bacteria and archea), a process in which alternative oxidants such as nitrate, sulfate, iron, manganese, and carbon dioxide are the terminal electron acceptors; and (iii) fermentative reactions, a process in which units of cleaved organic molecules serve as both oxidants and reductants of these redox reactions (Heip et al., 1995). Net organic matter production is also influenced by the balance between import and export of organic matter

from adjacent ecosystems (e.g., animal migrations included) because substantial inputs or outputs of labile organic matter can influence ecosystem respiration.

The methods used to measure ecosystem metabolism have developed substantially over the past century. Dissolved O_2 concentrations were widely used since the early twentieth century in bottle or chamber experiments to estimate metabolic processes in aquatic systems (e.g., Gaarder and Gran, 1927). This was because the release of O_2 during photosynthesis and uptake during aerobic respiration allows one to trace these processes with O_2, which can be measured with low cost and effort. Building upon approaches used in studies of coral reefs (e.g., Sargent and Austin, 1949), daily variations in O_2 concentrations of the water column at two stations in flowing waters were used to estimate ecosystem photosynthesis and respiration (Odum and Odum, 1955; Odum, 1956; Odum and Hoskin, 1958); a one-station method can also be applied in bays and estuaries (Caffrey, 2004).

Similar approaches were developed to measure carbon metabolism using daily variations in total carbon dioxide (TCO_2) concentrations (Ziegler and Benner, 1998) because TCO_2 changes capture both aerobic and anaerobic metabolism. Monitoring of the inorganic carbon system is especially useful in systems dominated by reef-forming organisms, where both organic matter processing and calcification can be quantified. Increasingly affordable and reliable sensors and instruments allowed this approach (both O_2 and TCO_2) to be used widely since the 1970s in varied coastal ecosystems, including shallow coastal bays (Caffrey, 2004), coral reefs (Odum and Odum, 1955), and seagrass beds (D'Avanzo et al., 1996; Gazeau et al., 2005b). Using modeling and budget analyses of inorganic nutrients and organic carbon, a series of related methodologies evolved for estimating net ecosystem metabolism for virtually any estuarine ecosystem (Smith, 1991; Testa and Kemp, 2008). More recently, continuous measurements of air–sea CO_2 exchange were achieved in diverse coastal environments (Gattuso et al., 1999), as well as the application of several approaches using various oxygen isotopes (Sarma et al., 2005; Tobias et al., 2007).

Research over the past half century demonstrated a range of applications of ecosystem metabolic rate measurements for a diversity of coastal ecosystems, many of which provide insight into the controls on metabolism. In general, rates of ecosystem production of organic matter are stimulated by increases in sunlight (also water clarity) and inorganic nutrient concentrations, causing ecosystem production to be sensitive to external nutrient inputs. In contrast, ecosystem respiration tends to be enhanced by higher levels of both water temperatures and labile organic substrates (Pomeroy and Wiebe, 2001); thus to some degree, organic matter production and consumption are controlled by different external forces. Net ecosystem production in shallow, clear waters tends to be higher if benthic plants that maintain large aggregations of plant biomass dominate; however, this is not true of coral reef ecosystems because ecosystem production and respiration tend to be in balance (Smith and Gattuso, 2009). Metabolic rates are generally depressed by toxic compounds from natural or human sources; however, anthropogenic contaminants (e.g., herbicides, fungicides, and insecticides) exert different effects on plants, microbes, and animals and thus shift the balance between ecosystem production and respiration (Wiegner et al., 2003). Measurements of ecosystem metabolism provide the quantitative information needed to balance food web models (Green et al., 2006) and to partition biogeochemical processes among various aerobic and anaerobic pathways (e.g., Hopkinson et al., 1999). Ecosystem production–respiration imbalances over time and across space provide an understanding of the timing and location of surplus organic matter production, which may support the development of hypoxic and anoxic zones in coastal waters (Kemp and Boynton, 1992).

The overall aim of this chapter is to provide an introduction and overview of the concepts, methods, and ecological relevance of organic matter production and respiration in estuarine and coastal ecosystems, with an emphasis on temperate latitudes. We also refer the reader to several excellent reviews of ecological or biogeochemical aspects of coastal ecosystem metabolism and the future challenges for the field, including Smith and Hollibaugh (1993); Heip et al. (1995); Gattuso et al. (1998); Smith et al. (2005), and Stæhr et al. (2011). In this chapter, we not only summarize these reviews but also extend them by (i) describing spatial and temporal variations in ecosystem metabolic rates and thus the important driving variables, (ii) describing various aspects of ecosystem metabolism in four case study ecosystems, (iii) summarize studies of cross-system comparisons, and (iv) discuss future research problems associated with measurements of aquatic ecosystem metabolism.

15.2 BASIC DEFINITIONS AND CONCEPTS

There are many terms commonly used to describe measured or computed rates of ecosystem-level primary production and respiration. Chamber incubations (in light and dark) and open-water observations of diel variations in metabolite concentrations (e.g., O_2, TCO_2) measure, during the daylight, rates of *apparent net daytime production* (P_a, per hour), which is generally assumed to be the difference between *gross primary production* (P_g) and *respiration* (R) during the day. Changes in metabolite concentrations observed in dark incubations are often assumed to be the same as those observed *in situ* at night, and these are referred to as *nighttime* (or *dark*) *respiration rates* (R_n, per hour). Changes in TCO_2 must be corrected for the contribution of $CaCO_3$ precipitation and dissolution in coral reef and other calcifying systems. If it is assumed that nighttime respiration rates are equal to daytime rates, they can be extrapolated to estimate 24-h respiration rates (R, per day). *Gross primary production* (P_g), which is defined as the total autotrophic production of organic carbon via fixation of TCO_2, is extremely difficult to measure directly (Sarma et al., 2005). In principle, P_g includes both photosynthetic and chemoautotrophic production of organic matter; however, the latter rates are generally assumed to represent a small contribution for most coastal ecosystems. Nevertheless, the operational definition of gross primary production, or *gross photosynthesis*, (P_g, per day) is assumed to be equal to $\alpha * P_a + (24 - \alpha) \times R_n$, where α is the number of hours of daylight (dawn to dusk) in the full 24-h day. Box 15.1 provides the definition of various terms used in the literature to describe the components of ecosystem metabolism. Many such terms are linked specifically to a particular method, while others are specific to particular components of the ecosystem (e.g., water column). Other terms include net community production (NCP), which is the net organic matter production of an ecosystem compartment (e.g., plankton, benthos), and gross oxygen production (GOP), which is the measurement of gross photosynthesis from the triple isotope method.

Metabolic rates (e.g., P_a or R_n) are often estimated by measuring changes in any reactant or metabolite involved in primary production and respiration of organic matter. For example, because O_2 is a product of photosynthesis, the quantitative increase in O_2 concentrations in a bottle over a given time represents a net photosynthetic rate for the plants within the bottle. Measurements made using changes in concentrations of O_2 or TCO_2 can be converted between O_2 and carbon rates using an assumed or measured photosynthetic quotient (i.e., the ratio of O_2 produced/TCO_2 fixed, ranging from PQ = 1.0–1.5; Box 15.1) and respiratory quotient (RQ = 1–1.3 for aerobic conditions, which is the ratio of TCO_2 released/O_2 consumed in respiratory processes (e.g., del Giorgio and Williams, 2005). Similar fixed stoichiometry for inorganic nutrients and other elements (N, P, S, Fe) and metabolic gases (O_2, TCO_2) are often assumed for ecosystem metabolism methods based on mass-balance calculations of the nutrients at large time/space scales (Smith, 1991; Testa and Kemp, 2008) or measurements of anaerobic metabolism (Kemp et al., 1997). Other methods are available for measuring metabolic rates of ecosystem components (e.g., plankton or benthos) using isotopically labeled reactants or metabolites, including $T^{14}CO_2$, $^{18}O_2$, or $^{15}NH_4^+$ (Peterson, 1980; Gazeau et al., 2007). Following calls to better understand the contributions of particular organisms to ecosystem metabolism, there has been interest in partitioning ecosystem respiration between the photosynthetic organisms (i.e., the *autotrophs*) and the nonphotosynthetic (i.e., *heterotrophic*) organisms (e.g., bacteria, zooplankton). Constraints in methodology have, however, limited the ability to make these distinctions.

Ecosystem metabolism studies are implicitly concerned with organic carbon balance, but metabolic properties are generally measured by tracing the uptake and production of inorganic carbon or dissolved oxygen. In most cases, especially under aerobic conditions and when $CaCO_3$ precipitation/dissolution is trivial, inorganic-carbon and oxygen-based measurements of primary production and respiration are equivalent (Gazeau et al., 2007) or can be converted using relatively consistent quantitative conversion factors (PQ and RQ). However, under anaerobic (no oxygen) conditions, a suite of alternative electron acceptors may be used in the decomposition of organic matter (Froelich et al., 1979), including, but not restricted to, nitrate (NO_3^-), oxidized forms of iron and manganese, and sulfate (SO_4^{2-}). These reactions generate CO_2 but do not consume oxygen directly, and as a result, O_2 measurements cannot be used to measure these respiratory processes. One particular reaction of interest is denitrification, a process in which nitrate is used as the terminal electron acceptor. This anaerobic process converts NO_3^-, which is a bioavailable inorganic nitrogen ion, into N_2, a gas that escapes into the atmosphere (Seitzinger, 1988), resulting in the loss of fixed nitrogen from aquatic ecosystems. This process does, however, generate

phosphate during organic matter decomposition, thereby altering DIN/DIP (dissolved inorganic nitrogen/dissolved inorganic phosphorus) ratios, which may influence primary production or algal speciation. Sulfate reduction, a process in which SO_4^{2-} is used as the terminal electron acceptor, is also of importance because bottom waters and deeper sediments in some estuaries are commonly devoid of O_2, yet rich in SO_4^{2-}, making sulfate reduction the major respiratory reaction during some seasons (Marvin-DiPasquale and Capone, 1998).

Other measures of metabolic rates are used as indices of the balance between photosynthesis and respiration of organic matter for entire communities and even ecosystems. These indices include the net organic matter production by the ecosystem, or *net ecosystem production* (per day), $P_n = (\alpha P_a) - (\beta R_n)$, where β is the number of hours of darkness (dusk to dawn) in a full day (Box 15.1). Positive values of P_n indicate a net surplus of organic matter and are referred to as *net autotrophic* conditions, while negative P_n values indicate a net deficit of organic matter and are called *net heterotrophic* conditions. This production/respiration balance can also be indexed by the ratio of the two measured rates; these "P/R ratios" can be expressed as (P_a/R_n), $(P_g - R)$, or $(\alpha P_a) - (\beta R_n)$. For convenience, in this chapter, we will use P/R to indicate the general ratio of P_g and R unless otherwise specified. This concept of metabolic balance has a long history in coastal and marine science, including an emphasis on the related *f-ratio* (ratio of phytoplankton production fueled by "new" external nutrient (e.g., NO_3^-) inputs to that fueled by internally "recycled" nitrogen (e.g., NH_4^+) generated from planktonic respiration (Quiñones and Platt, 1991).

Ecosystem metabolism represents the net effect of both physical and biological processes that contribute to organic carbon balance in coastal aquatic ecosystems. Ecosystem metabolism measurements quantify the "trophic status" of aquatic ecosystems, measured as both the metabolic richness and balance. Values of P_g and R reflect a system's richness in terms of nutrient and organic carbon pools, respectively. Alternatively, P/R and P_n reflect a system's status with respect to steady state balance between anabolic and catabolic processes (Odum, 1956), indicating a system's tendency to import or export organic material. Trends in annual indices of ecosystem metabolism follow changes in anthropogenic nutrient inputs and other indices of trophic state for mesocosms (Oviatt et al., 1986) and estuaries (Testa et al., 2008) because increased autotrophy is associated with elevated nutrient levels. Ecosystem metabolism in estuaries also reflects regional patterns of trophic status that tend to vary along the salinity continuum (Heath, 1995; Garnier and Billen, 2007), which is analogous to and functionally associated with concepts from river and stream ecology, including the river continuum concept (RCC, Vannote et al., 1980) and nutrient spiraling (Newbold et al., 1981).

Simple diagrams of ecosystem P_g versus R can be used in comparative analysis of trophic status (Fig. 15.1; Odum, 1956). Along the $P_g = R$ diagonal line, the system's metabolic state ranges from low rates in systems referred to as *oligotrophic* (with low nutrients and organic carbon) to high rates in systems called *eutrophic* (with high nutrients/organic carbon; Fig. 15.1). Above the diagonal line, ecosystem metabolism is net autotrophic, and below the line, systems are net heterotrophic. Changes in trophic

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BOX 15.1   Definitions and measures of ecosystem metabolism

For autotrophic communities only:

Autotroph	= plant or protists that produces organic matter from CO_2
Gross primary production (P_{atr})	= total photosynthesis in a plant or group of autotrophic organisms
Respiration (R_{atr})	= respiration of autotrophic organisms
Net primary production (P_{atr})	= $P_{atr} - R_{atr}$ = net organic matter production by autotrophic organisms

For ecosystem metabolic rates:

Net daytime production (P_a)	= net organic matter production by an ecosystem during sunlit hours
Nighttime respiration (R_n)	= respiration of an ecosystem during night hours
Gross primary production (P_g)	= total amount of photosynthesis in an ecosystem (often assumed = $P_a + R_n$)
Ecosystem respiration (R)	= total amount of respiration in an ecosystem
Net ecosystem production (P_n)	= $P_g - R = P_a - R_n$ = net organic matter production of all ecosystem components

Key ratios:

P/R ratio	= ratio of photosynthesis to respiration
Photosynthetic quotient (PQ)	= ratio of O_2 produced/CO_2 consumed in photosynthesis
respiratory quotient (RQ)	= ratio of CO_2 produced/O_2 consumed in respiration
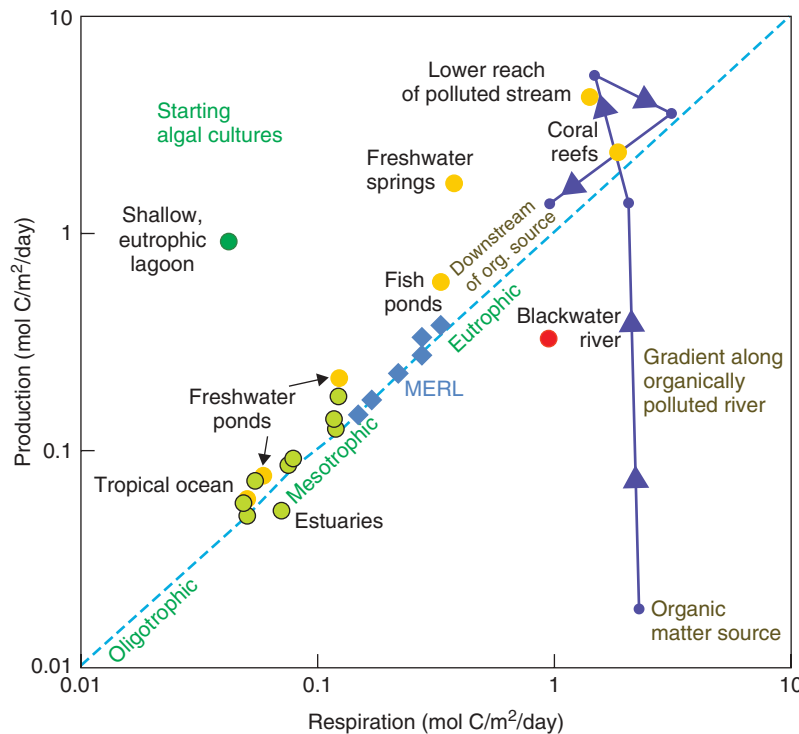
FIGURE 15.1 Regression of ecosystem respiration and ecosystem gross primary production across many types of aquatic ecosystems. Gross production and respiration tend to be balanced across many ecosystems types, including estuaries, but note that some ecosystems deviate from the 1:1 line substantially. Metabolic rates collected from various literature sources: nonestuarine systems (Odum, 1956), estuaries (Randall and Day, 1987; Day et al., 1988; Flores-Verdugo et al., 1988; Teague et al., 1988; Twilley, 1988; Hoppema, 1991; Heath, 1995), MERL nutrient enrichment experiment (Oviatt et al., 1986), blackwater river (Caffrey, 2004), shallow, eutrophic lagoon (D'Avanzo et al., 1996). *Source*: Based on Figure 8 in Odum (1956).

state along the diagonal represent changes in productivity, respiration, or general stimulation of metabolic processing, either via stimulation with additions of limiting inorganic nutrients or labile organic material (Fig. 15.1). Changes in state that are perpendicular to the diagonal reflect metabolic imbalances, for example, P_g greater than R in eutrophic, benthic-dominated ecosystems or beginning algal cultures, where ample light and nutrients generate short-term organic matter surpluses (Fig. 15.1). Conversely, R greater than P_g in rivers receiving high amounts of anthropogenic organic matter (e.g., blackwater rivers), where photosynthesis is highly light limited and respiration is fueled by high organic matter inputs (Fig. 15.1). In other rivers, upstream heterotrophy near the organic matter injection point often gives way to autotrophy in downstream waters, where there is less organic matter, abundant nutrients, and often clearer water (Fig. 15.1). At large time and space scales, ecosystem P_g and R tend to move toward a balanced condition ($P/R = 1$) because primary production yields organic matter that fuels respiration, while respiration releases inorganic nutrients that

stimulate production (Fig. 15.1). Consequently, P_g and R can fall out of balance over shorter time periods, with pulsed inputs of P_g-stimulating nutrients or R-stimulating labile organic material.

15.3 MEASURING ECOSYSTEM METABOLISM

The methods used to measure or calculate metabolic rates in coastal ecosystems span a range of spatial and temporal scales from liters and minutes for container incubations to cubic kilometers and multiple years for computations from whole system mass balances. Small-scale rate measurements tend to be more controlled and precise but more difficult to extrapolate to annual or interannual periods over entire ecosystems. In contrast, large-scale rates estimated from aggregated models and mass balances, while appropriate for the scales of whole ecosystems, are generally difficult to interpret for controlling factors and contributions from constituent habitats or functional groups. In this section, we briefly review the
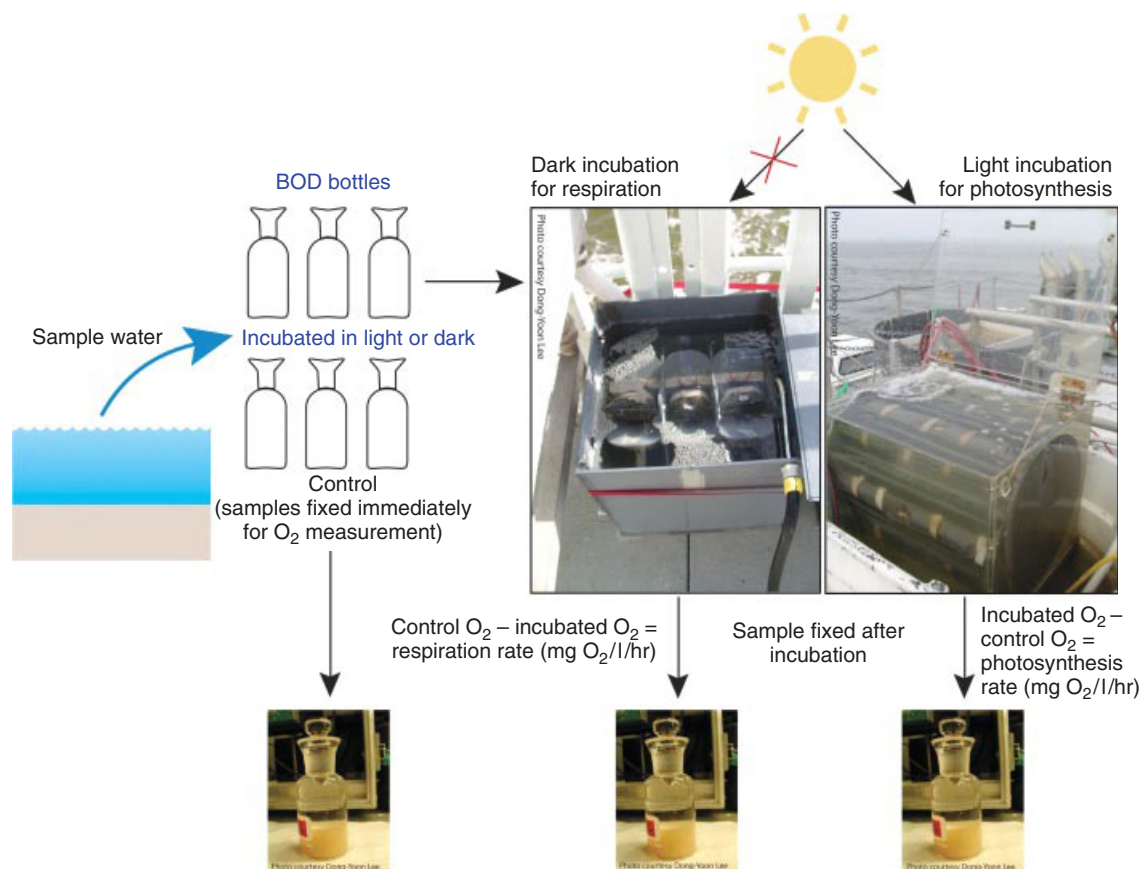
FIGURE 15.2   Measuring planktonic metabolism.

range of techniques that are used to estimate primary production and respiration for estuarine and coastal ecosystems and compare and contrast the scales, advantages, and disadvantages of each method.

15.3.1 Container Incubations

Perhaps the most common method to measure photosynthesis and respiration rates in aquatic ecosystems is by monitoring temporal changes in concentrations of key metabolites (O_2, TCO_2, particulate organic carbon (POC), inorganic nutrients) in enclosed chambers. Current technologies allow for precise measurements of metabolite concentrations and associated detection of low metabolic rates, including O_2 concentrations (Kana et al., 1994; Glazer et al., 2004) and TCO_2 and pCO_2 (Borges et al., 2004). Changes in O_2 or TCO_2 measured in bottles of sample water incubated at different light levels are used to infer rates of apparent daytime primary production and respiration (Gaarder and Gran, 1927; Gazeau et al., 2005a; del Giorgio and Williams, 2005). Figure 15.2

shows a schematic illustration, where dissolved oxygen (O_2) changes in bottle incubations are used to measure plankton community production and respiration. Water samples are collected and transferred to clear glass bottles (often called *BOD bottles* and usually 60, 125, or 300 ml in volume). For each depth and station, replicate bottles are ''fixed'' immediately, and the dissolved O_2 in the bottle is converted into a solid compound via the Winkler titration (Fig. 15.2). These bottles will provide the initial O_2 concentration. Another set of bottles will be incubated in the dark for 2–24 h, after which O_2 is measured. The difference in O_2 between the mean of the dark-incubated bottles and that of the initial bottles will equal the plankton community respiration rate. Other triplicate sets of bottles will be incubated in a rotating carousel at various light levels for 2–24 h. Light level is usually reduced by wrapping the bottles in porous wire sheaths. The difference in O_2 between the light-incubated bottles and the initial bottles is equivalent to the net primary production rate ($=P_g - R$). Differences in $P_g - R$ under different light levels are

coupled to water column light availability measurements to quantify depth-integrated $P_g - R$. Required durations of bottle incubations are inversely related to both the expected ambient rates and the precision of measurement methods.

Rates of phytoplankton photosynthesis are also commonly measured via uptake of ^{14}C-labelled bicarbonate, and the two measures tend to be highly correlated, with rates measured by ^{14}C uptake being generally intermediate between rates of P_a and P_g measured with O_2 and TCO_2 incubations (Peterson, 1980; Williams, 1993). Areal rates of benthic community respiration and photosynthesis, which are generally measured in opaque or transparent (respectively) intact sediment cores removed for controlled incubation or *in situ* chambers inserted into ambient sediments, usually include a short (e.g., 5–25 cm) overlying water column that is sampled in a time series over the incubation period (Hopkinson and Smith, 2005; Sundbäck et al., 2006). Measurements of plankton P_a and R_n made in relatively large and deep coastal systems can be used to approximate total ecosystem metabolism. In shallower systems, however, vertically integrated rates of plankton and benthic community metabolism (measured in chambers) are sometimes combined to estimate whole-ecosystem rates of P_a and R_n (Kemp et al., 1997; Gazeau et al., 2005a). Measurements of variations in $\delta^{18}O$ of O_2 during bottle incubations have been used with mixed success to estimate P_g in plankton communities (Bender et al., 1987; Gazeau et al., 2007).

The container incubation approach has several important strengths and limitations. One advantage is that it allows direct partitioning of P_n into relative contributions of different habitats. Second, controlled incubations allow for measurements of P_a and/or R_n responses to variations in physical (e.g., levels of temperature, light, and salinity), chemical (e.g., nutrient levels), or biological (e.g., grazers and predators) conditions. This approach has two important limitations. First, one must either make numerous individual rate measurements over large spatial and temporal scales to adequately characterize variability within the system, which can be prohibitively resource demanding. Alternatively, limited individual measurements within the system must be extrapolated over large time and space scales to yield an integrated metabolic rate; these calculations introduce a series of individual errors that propagate to create a large and difficult-to-quantify level of uncertainty in the calculated ecosystem rate (e.g., Smith, 1991). Second, isolation of water within a closed space introduces what are called ''container effects,'' in which the isolated ecosystem unit (water, sediments, and organisms) changes over the incubation in artificial ways (e.g., predator isolation and algae growth on walls), which will alter the rate measurement itself. It may also be impractical to measure all compartments of a particular ecosystem.

15.3.2 Open-Water Changes in Metabolites

In systems with relatively homogeneous water masses (because of reduced mixing and/or slow water exchange), clear signals of diel changes in water-column O_2 and TCO_2 concentration are often detectable and associated with ecosystem metabolism (Fig. 15.3). Such a deployment scheme, in a well-mixed water column, will measure the integrated change in O_2 concentration due to photosynthesis and respiration of both water column and benthic organisms (Fig. 15.3b). For example, the rate of O_2 concentration increase during the day is equivalent to P_a and the rate of decline during the night is equivalent to R_n (Fig. 15.3c). The advantage of this approach is that it measures the integrated metabolic activity of the entire ecosystem over a short time period and that sensors can be deployed for weeks or more, allowing long-term measurements. The method, however, has the disadvantage of requiring an atmospheric exchange correction (which is difficult to measure accurately) and the possibility of low- or high-O_2 water being advected past the sensor, which will cause over- or underestimation of metabolic rates.

To derive rates of ecosystem P_a and R_n from changes in water-column metabolite concentrations, O_2/TCO_2 changes must be corrected for losses or gains via air–water exchange (Fig. 15.3d; e.g., Odum and Odum, 1955; Odum and Hoskin, 1958). This air–water gas flux is typically modeled as the product of a gas exchange coefficient (or piston velocity) and the difference between measured surface O_2 and calculated saturation concentrations. Values for the piston velocity, which generally increase with waves and turbulent mixing in surface water, are commonly computed from statistical relationships with wind speed and/or tidal currents (Wanninkhof et al., 2009; Borges and Abril, 2011), tracer additions (such as SF_6) that integrate variable turbulence and weather over several days (Clark et al., 1996; Carini et al., 1996), and direct measurements using floating domes (Kremer et al., 2003). In the absence of such measurements in comparative analyses of metabolism among similar systems, piston velocities are assumed to be constant (Caffrey, 2004), despite the fact that air–sea exchange is highly variable between systems.
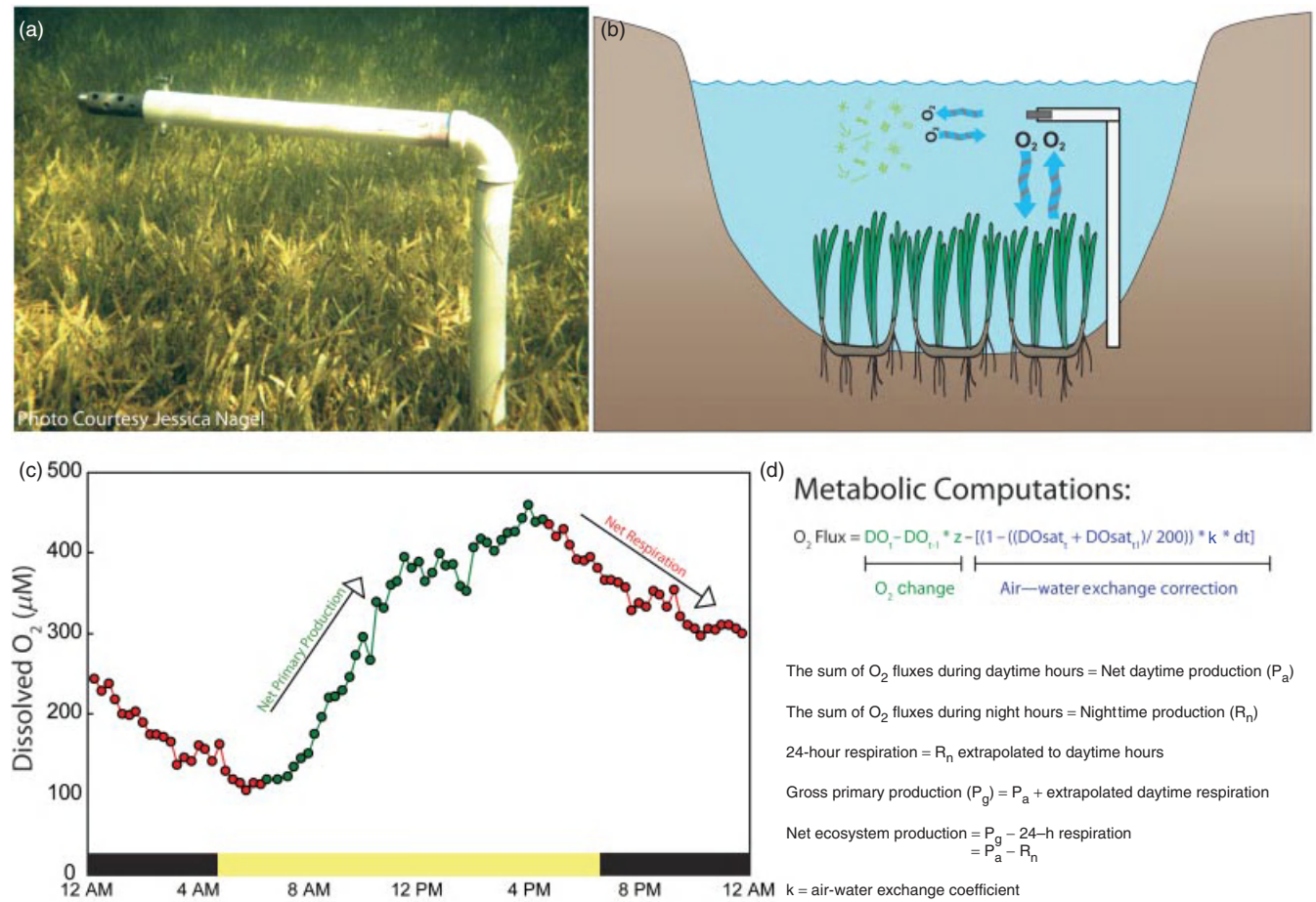
FIGURE 15.3 Measuring diel fluctuations in O_2 and computing metabolic parameters from O_2 time series.

In coastal ecosystems with well-defined uniform water flow during intervals of the tidal cycle, metabolic rates can, in concept, also be estimated using flow velocity and differences in concentration between an upstream and a downstream station (Odum, 1956). Rates of gross primary production can be inferred at broad spatial and temporal scales from the triple oxygen isotope (^{16}O, ^{17}O, and ^{18}O) composition of atmospheric and dissolved O_2 using independent estimates of air–water O_2 exchange (Luz et al., 1999; Sarma et al., 2005). Measurements of $\delta^{18}O$ are also used to estimate P_g, R, and $P_g : R$ separately in open waters over diel cycles (Tobias et al., 2007).

One advantage of the open-water technique is that long time series of O_2 concentrations can be measured with relative ease using modern sensor systems that are generally precise, durable, and self-cleaning. These sensor systems can be deployed remotely in coastal waters to provide high-frequency (e.g., 15-min intervals) observations for durations of weeks to months (Caffrey, 2004), allowing it to be the only method to provide direct measurements of ecosystem metabolism on a wide range of temporal and spatial scales. In addition, this open-water approach provides direct measurements of ecosystem-level production and respiration, thus avoiding artifact-associated ''container effects'' or rate extrapolation. Although this method does not provide habitat-specific metabolic rates, combining it with container incubations in a single study provides both direct measurements of whole system rates and their partitioning among subsystems (Smith and Hollibaugh, 1997; Kemp et al., 1997).

Among the disadvantages of this approach is the common need for separate measurements of air–sea O_2 (or CO_2) exchange to correct for an inherent bias toward lower rates (due to gas exchange). Direct measurements of air–water exchange for a specific system can be difficult to obtain (Raymond and Cole, 2001), and gas exchange often varies substantially from system to system (Kremer et al., 2003) and with fluctuations in physical forces (Marino and Howarth, 1993; Clark et al., 1996; Borges et al., 2004; Borges and Abril, 2011). In dynamic tidal waters, diel changes in O_2 may be masked by physical forces (air–sea exchange, vertical/horizontal mixing and advection), making it difficult to detect the metabolic signal. Statistical modeling of relationships among O_2, CO_2, water temperature, and/or salinity can provide a means for inferring metabolic rates in systems in which the time–space variability due to physical processes is substantial (Swaney et al., 1999; Lee, 2001). Much like container incubations, metabolic rates derived from open-water time series O_2 measurements only represent a small area such that estimates for large dynamic estuarine systems with strong horizontal gradients require spatial arrays of numerous sensor systems (Martz et al., 2008). Last, in using open-water changes in O_2 and TCO_2 concentrations as measures of ecosystem metabolism, one must also account for the potential import of waters from adjacent habitats that are either super- or undersaturated, thus leading to biased air–sea exchange corrections.

15.3.3 Direct Air–Water Gas Exchange

Another approach for estimating P_n in aquatic systems is to measure or compute the air–sea exchange (F_{aw}) of O_2 or CO_2 over sufficient time and space to characterize the entire ecosystem. At steady state, a net efflux of O_2 and net influx of CO_2 indicate positive values of P_n (and vice versa). Direct field measurements of F_{aw} based on changes in O_2, CO_2, or inert tracer gases can be made in an enclosed atmosphere under floating chambers (Odum, 1956; Frankignoulle, 1988). The product of empirically estimated piston velocities (γ) and the difference between saturation and measured O_2 or CO_2 concentrations in surface waters ($F_{aw} = \gamma(C_s - C)$) provides an estimate of F_{aw} adequate for correcting P_a and R_n rates inferred from daily changes in gas concentration (e.g., Raymond and Cole, 2001; Kremer et al., 2003). Alternatively, direct estimates of P_n can be made from F_{aw} with precise calculations of dissolved gas partial pressure at the very surface (skin) of the water column (e.g., Najjar and Keeling, 2000). Spatial interpolations of monitoring data and numerical model output generate climatologies of O_2 or CO_2 partial pressure and physical conditions to estimate seasonal patterns of P_n for large systems (Najjar and Keeling, 2000; Cai et al., 2006).

15.3.4 Input–Output Budgets

At larger space and time scales, a range of mass-balance and budget approaches can be applied for computing rates of P_n in coastal ecosystems. The most straightforward of these approaches includes steady state nutrient, organic carbon, and/or O_2 input and output budgets that are based on flux estimates for each material across system boundaries. The boundary fluxes can be measured and/or derived from simulation models. In this case, P_n is often computed as the residual of the mass balance. For estuaries and other semienclosed coastal systems, values of P_n can be inferred from measurements of differences between input and output fluxes for organic carbon, O_2, or inorganic and organic nutrients (Chapter

17; Kemp et al., 1997; Smith et al., 2005). Metabolite inputs from the atmosphere and anthropogenic point sources (e.g., sewage effluents) are usually measured by routine monitoring programs (Carstensen et al., 2006). Inputs from diffuse watershed sources can generally be obtained from river monitoring at fall lines and/or hydrochemical modeling of runoff. Such point and diffuse inputs from the surrounding watershed are sometimes combined in mass-balance calculations. For most budget calculations, direct estimates of mass exchange fluxes between the estuary and adjacent ocean must be derived using hydrographic models of varying complexity (Boynton et al., 2008; Testa and Kemp, 2008) because measuring such fluxes is difficult.

15.3.5 Transport-Transformation models

A related approach for estimating values of P_n from mass balances involves computing net biogeochemical transformations of nonconservative solutes within a system using hydrodynamic models or steady state calculations of transport. These calculations are often applied to coastal systems with clear land–sea salinity gradients that permit transport computations using salt- and water-balance models (Smith et al., 1991; Gazeau et al., 2005a; Testa et al., 2008). This approach calculates the residual water fluxes between predefined volumes in systems in which freshwater inputs, salinity distribution, and system bathymetry are known. For nonconservative solutes (e.g., PO_4^{3-}), mass balance requires an additional residual term to represent the net effect of all biogeochemical processes involving the solute (Chapter 17). One approach for this kind of modeling focuses on calculating the net nonconservative production or consumption of DIP. In assuming that biological processes dominate phosphorus cycling, for example, net DIP consumption represents net biological uptake of DIP, which is converted to equivalent net carbon production assuming that stoichiometry is fixed (Smith et al., 1991). Thus, net DIP consumption is used to compute P_n. This approach has been supported by and widely used in the Land-Ocean Interaction in the Coastal Zone (LOICZ) project (Crossland et al., 2005). A related approach uses this method to balance nonconservative metabolic gases (e.g., O_2 or CO_2), also accounting for air–sea exchange to compute P_n (e.g., Smith and Hollibaugh, 1997; Testa and Kemp, 2008). A two-layer version of this approach, which can be applied for stratified estuarine systems, provides metabolic rates that are analogous (but not equivalent) to P_a in the upper photic layer and R in the subphotic bottom layer (Hagy et al., 2000; Testa et al., 2008).

An inherent strength for these mass-balance approaches is the fact that they are computed over large space and time scales, thus providing integrated measures of P_n that can be related to large time- and space-scale external forcing. These estimates of net ecosystem metabolic fluxes can also be quantitatively related to other large-scale carbon and nutrient fluxes in the ecosystem (Kemp et al., 1997). The conceptual simplicity of this approach combined with the widespread availability of monitoring data for constructing mass balances makes it an excellent tool for comparative analysis of P_n across many different coastal ecosystems (Smith et al., 2005). A potential limitation of the transport-transformation modeling approach is that it requires two key assumptions: (i) the C/N/P stoichiometry is fixed and known and (ii) physicochemical reactions have no net effect on DIP dynamics (Gazeau et al., 2005a). The primary disadvantage of all mass-balance approaches is that many measurements or computations are required to estimate P_n and some of these rates may be difficult to quantify and may have large associated errors. Problems of spatial and temporal extrapolation are minimized in systems with long water exchange times and relatively uniform conditions. The scales of the various flux estimates required for a complete mass balance must be consistent, must cover the same temporal period and spatial domain, and must be measured at frequencies and spatial densities adequate to reflect integrated rates. Although it can be difficult to quantify the errors and uncertainties in many of these measurements, recent studies describe rigorous approaches for computing error accumulation in these mass-balance calculations for nutrients and other materials (Lehrter and Cebrian, 2010).

15.4 REGULATING FACTORS AND SPATIAL/TEMPORAL PATTERNS

An appreciation of the various internal and external factors that regulate the balance between production and consumption of organic matter is necessary for understanding ecosystem metabolism. Many external and internal factors, both natural and anthropogenic, drive changes in estuarine metabolic rates, while spatial and temporal variations in these controlling factors result in distinct gradients and patterns in the rates. This section focuses on six factors that exert strong and ubiquitous control on coastal ecosystem metabolism in varied coastal aquatic ecosystems.
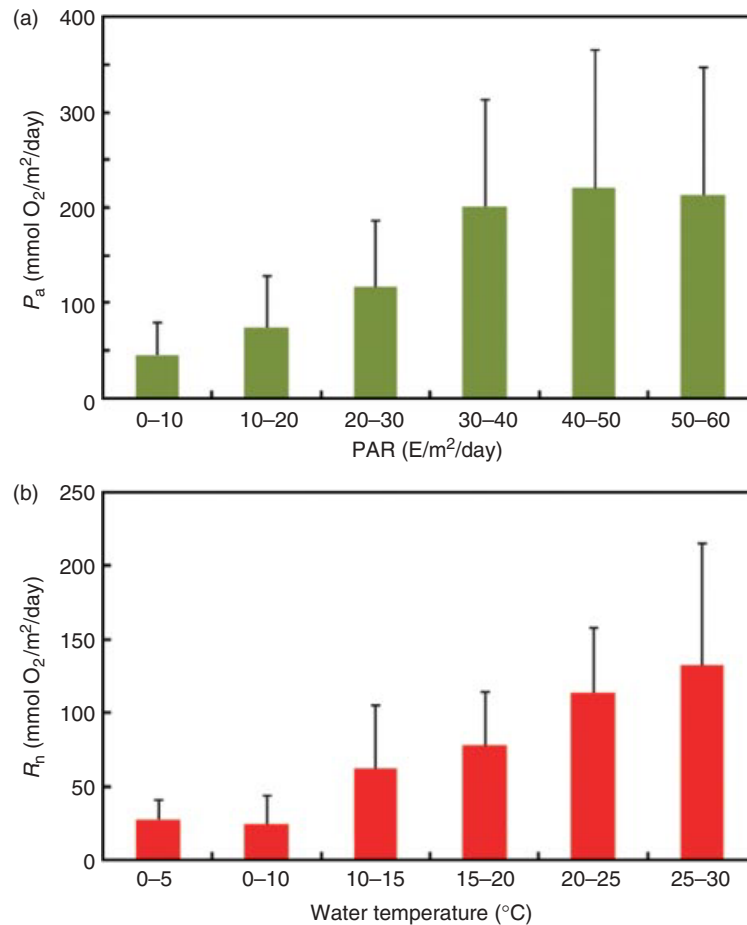
FIGURE 15.4 Plots of binned means ($\pm$SD) of (a) net daytime production (P_a) versus photosynthetically active radiation (PAR) and (b) nighttime respiration (R_n) versus water temperature in the Corsica River estuary, a subtributary of Chesapeake Bay. Metabolic rates were calculated from short-term changes in water column O_2 and represent whole-ecosystem metabolism. P_a correlates with PAR, but saturates at 30–40 E/m^2/day with high variability at high PAR, because of turbidity-induced reductions in P_a. R_n increases exponentially with temperature and does not appear to saturate up to 30 °C. *Source*: O_2 and temperature data from Maryland Department of Natural Resources (www.eyesonthebay.net) and PAR data from the Horn Point Laboratory weather station in Cambridge, Maryland, USA (http://hpl.cbos.org/download.php).

15.4.1 Light and Water Clarity

Primary production in coastal waters may be limited by nutrients, temperature, and mixing, but light availability is the ultimate driver of photosynthesis. Light energy is absorbed by a suite of plant pigments, notably chlorophyll *a*, and drives the light and dark reactions of photosynthesis to fix CO_2 and synthesize simple organic compounds. For example, rates of phytoplankton photosynthesis follow daily (e.g., Harding et al., 1981) and seasonal (e.g., Smith and Kemp, 1995) variations in solar intensity and duration (Fig. 15.4), especially in temperate climates (Smith and Hollibaugh, 1997; Hashimoto et al., 2006). Photosynthetic rates generally follow hyperbolic relationship with light up to saturation levels (Harding et al., 1981), where at higher light levels,

UV inhibition of photosynthesis is sometimes evident (Powles, 1984; see Chapter 4). Such photoinhibition of phytoplankton photosynthesis is rarely observed *in situ* in most coastal ecosystems because turbid water combined with rapid vertical mixing precludes long exposures to damaging light levels (Gallegos and Platt, 1985). As a result, simple empirical models are used to effectively compute phytoplankton productivity based on light availability, phytoplankton biomass, and photic zone depth across a range of diverse coastal ecosystems (Cole and Cloern, 1987).

As a result of light control on photosynthesis, the daily rising and setting of the sun fuels one of the most clearly observed metabolic cycles in coastal ecosystems. Net increases in O_2 during sunlit hours reflect

net ecosystem photosynthesis, while declines in O_2 during the night result from net respiration (Fig. 15.3). A common lag period (2–5 h) between dawn and the initial switch from net respiration to net photosynthesis (Fig. 15.3) reflects the time required for gradually increasing photosynthetic rate to exceed baseline respiration rates. Direct bottle incubation measurements of plankton community photosynthesis and respiration indicate that midday maxima in P_g are typically followed by respiration peaks in late afternoon. Late afternoon peaks in respiration rates, however, may be driven by light enhancement of respiration associated with high ratios of $O_2 : CO_2$ concentrations.

Water clarity is a critical factor influencing light availability and photosynthesis that varies widely among coastal ecosystems. In natural waters, the intensity of light reaching below-surface depths is reduced rapidly due to absorption and scattering by algal cells (live and dead) and a variety of nonalgal suspended inorganic and organic particles in the water column (Wofsy, 1983). Consequently, photosynthetic rates and the accumulation of phytoplankton chlorophyll *a* are often reduced in estuaries receiving high loads of inorganic particles and/or allochthonous organic material (Wofsy, 1983; Kemp et al., 1997). Photosynthesis in benthic plants is especially sensitive to decreases in water clarity (McGlathery et al., 2007) because unlike phytoplankton, benthic algae and submersed vascular plants are attached to sediments and their depth limit is controlled by light penetration. P_g is thus often lower in regions of estuaries nearest the injection point of riverine turbidity (e.g., upper, low-salinity estuarine regions; Smith and Kemp, 1995; Gazeau et al., 2005c) and during years or seasons with high river flow and suspended sediment inputs, such as temperate spring months and tropical monsoon periods (Ram et al., 2003).

Although respiration in coastal ecosystems is generally not directly affected by light levels, two processes can cause elevated plant respiration in the light. The first process, photorespiration, occurs in many plants when low intracellular concentrations of CO_2 allow O_2 to bind with RuBisCO to form glycolic acid. This material may be respired within the plant or excreted to surrounding waters, where it used in microbial respiration (Laws et al., 2000). A second process by which O_2 consumption and CO_2 production may be stimulated in the light is the Mehler reaction (Raven and Beardall, 2005). Experiments suggest that the sum of these two processes of light-stimulated respiration probably account for less than 20% of P_g (Laws et al., 2000). Dark bottle respiration rates measured with incubations over diel cycles (Sampou and Kemp, 1994) suggest that midday rates exceed nighttime rates. However, over longer time periods (> day), high light conditions generally increase respiration indirectly by stimulating photosynthesis, which provides both organic substrate and O_2 to support elevated aerobic respiration. In benthic environments, photosynthesis by benthic microalgae and submersed vascular plants increases the depth of O_2 penetration into sediments, resulting in elevated aerobic respiration and chemoautotrophic metabolism (Epping and Jørgensen, 1996).

15.4.2 Temperature

Temperature has a strong effect on respiration, because of its influence on enzyme-catalyzed cellular metabolism. Metabolic rate dependences on temperature are expressed as the ratio of rates at a given temperature and those at $10\,°C$ greater, which is called the ''Q_{10}'' factor (Chapter 3). A number of comparative analyses show that respiration of both planktonic and benthic communities follow strong exponential relationships to temperature (Hopkinson and Smith, 2005), which indicates that Q_{10} should be dependent on the magnitude of temperatures being compared (i.e., a Q_{10} for 5–15 $°C$ will be lower than that for 15–25 $°C$). Such temperature–respiration relationships were reported for a diversity of coastal ecosystems (Fig. 15.4; Smith and Kemp, 1995), and strong correlations between temperature and respiration also result from covariance between temperature and primary production rates. In the latter case, increased productivity increases the availability of labile organic matter to fuel respiration. In deeper, aphotic waters, respiration may peak with temperature (as in surface waters), and in many temperate ecosystems, peak benthic respiration co-occurs with peak temperature (e.g., Middelburg et al., 1996). Organic matter reactivity is thought to be more important than temperature in regulating respiration rates (Satta et al., 1996), especially in systems with large inputs of organic matter from terrestrial and anthropogenic sources, in sediments that are dependent on sinking organic material to support respiration (Graf et al., 1982), and in sediments in which elevated abundance of macrobenthic fauna enhances respiration rates (Hopkinson and Smith, 2005).

Seasonal and interannual temperature fluctuations can directly and indirectly affect rates of P_a and P_g in coastal ecosystems. Although the photochemical processes in photosystems I and II and the initial slope of light-saturation curves (Platt and Jassby, 1976) are generally unaffected by changes in temperature, temperature tends to set the maximal growth rates (μ_m) of phytoplankton under ideal light and

nutrient-saturated conditions (Eppley, 1972). Modeling studies similarly found that simulation performance was generally improved by using formulations for temperature-dependent μ_m rates that included modulation by light and nutrient conditions (Brush et al., 2002).

Temperature also exerts indirect effects on primary production, as planktonic and benthic nutrient recycling rates are generally enhanced in warmer water, potentially increasing the growth rate of nutrient-limited phytoplankton and benthic plants (Heip et al., 1995). Although coastal phytoplankton (and other plants) tend to adapt to local conditions, extremely high temperatures (>30 °C) can inhibit plant growth (Eppley, 1972). It is generally considered that ecosystem respiration is more sensitive to temperature (as reflected in higher Q_{10} values) than system photosynthesis. Consequently, global increases in water temperature are expected to cause widespread reductions in P/R ratios and increased heterotrophy for oceanic and coastal systems (López-Urrutia et al., 2006).

Both P_g and R are strongly influenced by (and correlate with) seasonal variations in temperature, whereas temperature effects on seasonal or interannual fluctuations in P_n are often difficult to detect. In many temperate estuaries, P_g may follow the annual light cycle (peaking in June), while ecosystem respiration tends to follow the annual temperature cycle (peaking in July or August), resulting in spring annual maxima in P_n (Smith and Kemp, 1995). Conversely, in estuaries with seasonal climate patterns driven by the monsoon cycle, P_n may be autotrophic during low-flow, premonsoon periods but may be reduced to heterotrophic conditions during high flow (and high allochthonous organic matter inputs), monsoon periods (Ram et al., 2003). Thus, year-to-year variations in P_n may be related to a variety of factors other than temperature, as interannual variability in temperature is small relative to changes in other external forces (e.g., turbidity, nutrient inputs).

15.4.3 Inorganic Nutrients, Organic Carbon, and Toxic Contaminants

In many coastal ecosystems, photosynthetic production and respiratory consumption of organic matter are regulated by both inorganic nutrient and organic matter inputs. Typically, variations in land–sea input rates are driven by climatic variability or anthropogenic forcing (Smith and Hollibaugh, 1997; Testa et al., 2008; Cox et al., 2009), as changes in freshwater inputs and watershed land use control input rates. As a result of combined anthropogenic and climatic forcing, input rates vary on seasonal to multidecadal

timescales. Primary production (both P_a and P_g) rates are often positively correlated with inorganic nutrient inputs in many types of aquatic ecosystems, as nutrients increase photosynthesis levels and allow for increased algal biomass production (Oviatt et al., 1986; D'Avanzo et al., 1996; Caffrey, 2004). For example, controlled multiyear experiments in mesocosms displayed that a 32-fold increase in inorganic nutrient input elicited a significant increase in P_a and P_n (Oviatt et al., 1986). Such elevated organic production, in turn, induces elevated respiration rates, because much of the newly produced organic matter will likely be respired within the time frame of a year (Oviatt et al., 1986; Smith and Hollibaugh, 1997; Hashimoto et al., 2006). Respiration rates vary substantially with changes in external loads of organic matter (Satta et al., 1996; Smith and Hollibaugh, 1997), especially in upstream regions of estuaries adjacent to wastewater treatment plants and riverine injection points (Gazeau et al., 2005a). In some systems, ecosystem metabolism is driven by organic matter (Smith and Hollibaugh, 1997) or inorganic nutrient inputs (Testa et al., 2008) from seaward sources.

The ratio of inorganic nutrient to organic matter inputs is a predictor of P_n and P/R for many coastal systems (Fig. 15.5; Hopkinson and Vallino, 1995; Kemp et al., 1997; Gazeau et al., 2005a) because inorganic nutrients directly stimulate P_g and organic nutrients fuel ecosystem respiration. For example, ecosystem metabolism in Tomales Bay is net heterotrophic and the system is thus a sink of organic carbon and source for CO_2. This is because the estuary's small watershed is sparsely populated but delivers substantial terrestrial organic carbon and little inorganic nutrients to the adjacent bay (Smith et al., 1991; Smith and Hollibaugh, 1997). However, the Scheldt River estuary has negative P_n despite high inorganic nutrient loads, because of light limitation and excessive inputs of allochthonous organic material (Gazeau et al., 2005a). Narragansett Bay, in contrast, receives higher loads of inorganic nutrients than organic carbon from its watershed, and ecosystem metabolism is slightly autotrophic in this system (Fig. 15.5; Nixon et al., 1995). The Patuxent River estuary is highly enriched with inorganic nutrients and is autotrophic, but interannual variability indicates shifts between autotrophy and heterotrophy caused by variations in other external forces (Testa et al., 2008).

The effect of organic matter inputs on the metabolic balance of coastal waters depends largely on the bioavailability and elemental composition of this material. In general, organic matter produced by phytoplankton and benthic microalgae tends to
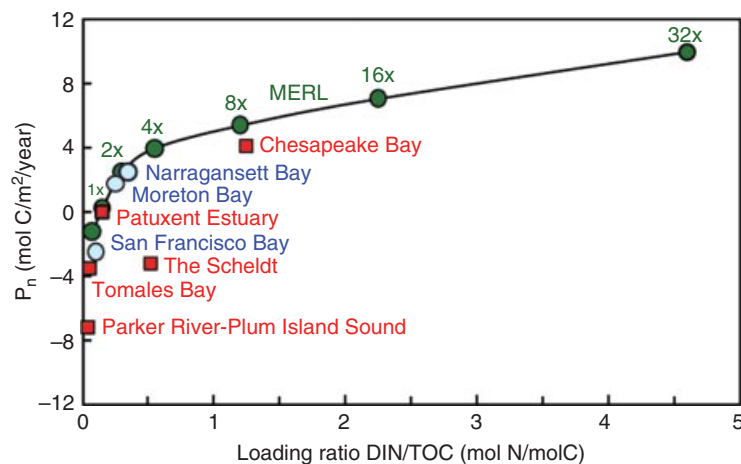
FIGURE 15.5 Comparative analysis of net ecosystem metabolism for estuarine systems in relation to the loading ratio of DIN/TOC (dissolved inorganic nitrogen/total organic carbon). Data from experimental marine ecosystems (green, filled circles, MERL, Oviatt et al. (1986), C = control and 1X, 2X, etc. are scales of nutrient enrichment relative to control), selected estuaries for which sufficient information is available (blue, open circles, Kemp et al. (1997)); Moreton Bay from Eyre and McKee (2002), and the case study systems from this chapter (red squares), including the Patuxent River estuary (Testa et al., 2008), Chesapeake Bay (Kemp et al., 1997), the Scheldt (Hofmann et al., 2008), Tomales Bay (as in Kemp et al., 1997), and the Parker River-Plum Island Sound ecosystem (Vallino et al., 2005).

be very labile (high bioavailability) with relatively low molar ratios of C : N ($\sim$7) and C : P ($\sim$106), so that respiration of 106 moles of C will result in release of 16 moles of inorganic N and 1 mole of inorganic P. In contrast, organic material produced by seagrass and salt-marsh grass tends to be more refractory with higher C/N ratios ($\sim$20 and $\sim$40, respectively) because a larger portion of the plant biomass is associated with structural tissues (e.g., Twilley et al., 1986). Without the buoyancy effects of water, terrestrial plants have even more biomass devoted to structural carbon and C/N ratios can exceed 150 (Cloern et al., 2002). Although cellulose, lignin, and other structural compounds tend to be relatively resistant to degradation, they do support respiration of bacteria and fungi, but with very small relative rates of inorganic nutrient release. Inputs of allochthonous terrestrial organic matter thus tends to support lower respiratory rates that release far less inorganic N and P, compared with a similar input of algal-derived organic matter produced by phytoplankton. Therefore, increased inputs of terrestrial organic matter generally increases estuarine respiration with relatively little effect on photosynthesis from associated nutrient recycling, whereas enhanced inputs of organic matter from algal-derived material will tend to increase both R and P while driving a net increase in heterotrophy.

Inputs of toxins to coastal ecosystems may also affect P_n, P_g, and R. The toxicological literature is filled with data on experimental ecosystem metabolic responses to diverse organic and inorganic contaminants (Graney et al., 1994). Response patterns vary for different toxic chemicals, but there is a general concern that the homeostatic nature of ecosystem metabolism makes these rates poor indicators of low-level ecosystem stress. A recent study contrasting estuarine ecosystem metabolic responses to inputs of nutrients (N and P) and heavy metals (arsenic, copper, cadmium) reported that ecosystem production was significantly stimulated by nutrients and inhibited by metal toxins, while input of both sets of chemicals resulted in slight enhancement of P_g and P_n (Wiegner et al., 2003). In contrast, herbicide additions to seagrass-dominated mesocosms resulted in sharp declines in P_a that abated within weeks as the herbicides degraded (e.g., Cunningham et al., 1984). It is interesting that, despite these large impacts on P_a, community respiration showed little response to these phytotoxic compounds over the full course of 6–10 week treatments (Kemp et al., 1985). In rare cases, extreme levels of NH_4^+ may be toxic to phytoplankton and reduce P_a (Cox et al., 2009).

15.4.4 Exchanges of Organic Matter Within Ecosystems

Analyses of metabolic balance in ecosystems open to exchange (especially streams and macrotidal estuaries) must consider how organic material is exchanged between adjacent aquatic ecosystems. Measurements

of P_n can be used to estimate the direction and magnitude of organic transport across system boundaries, as organic matter is generally imported to fuel heterotrophic ecosystems and exported from autotrophic ecosystems at steady state. Of course, organic carbon export may be driven by a combination of both autotrophic P_n and the throughput of unused imported materials, but it is nonetheless useful to consider potential relationships between net biological production and net physical transport.

Several studies have linked net ecosystem production in upper euphotic layers of the water column to net *vertical transport* (i.e., sinking) of particulate organic carbon (POC) and to subsequent bottom respiration supported by these sinking organic materials. For instance, in stratified estuarine ecosystems, there can be a strong interannual correlation between net O_2 production in the surface layer and net O_2 consumption in the underlying layer (Testa and Kemp, 2008) and an analogous relationship between metabolism and POC deposition (Bozec et al., 2006). Direct measurements of P_n and sinking of POC were also strongly correlated in mesocosm experiments (Oviatt et al., 1993), field studies in estuaries (Kemp and Boynton, 1992), and on the North American continental shelf (Kemp et al., 1994). Perhaps the most important example of downward vertical sinking of surface water POC on a global scale is the potential export of newly fixed carbon to the deep oceans as part of the "biological pump" (Lutz et al., 2007).

Changes in P_n are also related to variations in net *horizontal transport* between adjacent coastal regions. For example, despite the high net autotrophy of the seagrass plants themselves, net heterotrophy is often observed for the integrated ecosystems associated with seagrass beds (Barron et al., 2004) because of the tendency for allochthonous POC to be trapped within the bed and respired by benthic microbes and metazoan communities. The box-modeling analyses described above (Bozec et al., 2006; Testa and Kemp, 2008) showed that regions of net autotrophy were often adjacent to regions of net heterotrophy and that seaward horizontal transport of excess production in the net autotrophic areas fueled heterotrophy in the downstream regions.

Net autotrophy in nutrient-enriched estuaries generally creates a source of organic matter that is transported seaward to fuel net heterotrophy on the adjacent shelf (Ram et al., 2003). However, landward transport of organic matter from autotrophic coastal upwelling areas can also drive heterotrophy in nearby estuaries (Smith and Hollibaugh, 1997). Previous conceptual models of "river to sea" interactions of organic matter and nutrient cycles have explained observed horizontal patterns of P_n along estuarine land−sea gradients in terms of linkages between P_n and net organic matter transport (Heath, 1995; Hopkinson and Vallino, 1995). Such estuarine-centric models can be related to the RCC (Vannote et al., 1980), which describes a pattern of heterotrophic low-order streams giving way to autotrophic high order river systems. It is suggested that forest cover in low-order streams has the dual function of restricting light to stream beds and providing ample amounts of organic material to fuel respiration, while higher-order streams receive nutrients from upstream respiration and are wide enough to provide ample light for photosynthesis, permitting net autotrophy. This pattern is intimately linked with the concept of "nutrient spiraling" in streams, where the autotrophic uptake and heterotrophic release of nutrients co-occurs with unidirectional, downstream flow, thus decoupling regions of organic matter degradation/nutrient release from those of organic matter production/nutrient uptake (Ensign and Doyle, 2006).

15.4.5 River Flow, Flushing, and Wind

Because many estuaries, by definition, receive freshwater (and thus organic matter and nutrient inputs) from one or many sources, variations in freshwater flow exert strong, if not dominant, controls over metabolic rates (Paerl et al., 1998; Howarth et al., 2000; Russell et al., 2006). Depending on the estuary and its watershed, interannual changes in river flow can increase or decrease metabolic rates or lead to spatial and temporal shifts in peak metabolism. In estuaries receiving large amounts of inorganic nutrients with river flow, elevated flow leads to increases in phytoplankton production (Paerl et al., 1998). Conversely, elevated river flow can lead to reduced P_g by importing suspended material that reduces light availability (Howarth et al., 2000). If the estuary is large enough, flow may reduce P_g via turbidity in landward estuarine regions while elevating P_g in seaward waters where dissolved nutrients are delivered, but solids settle to sediments in landward reaches. Large seasonal pulses of freshwater and organic material (monsoon) can also reduce P_g and P_n via light reductions and elevated respiration because of organic matter imports (Ram et al., 2003). More complex interactions occur in naturally turbid estuaries, where freshwater discharge can affect both water column stability and turbidity (Cloern et al., 1983; Howarth et al., 2000), and large stream-flow pulses can radically alter P_n with differential effects on P_g and R resulting from mixed inputs of dissolved

organic carbon (DOC) and/or turbidity (Russell et al., 2006).

Day-to-day fluctuations in P_g, R, and P_n are often large, because of daily variance in other external forcing variables, such as wind and sunlight. In the few instances when continuous daily measurements of P_n were reported over a season (Fig. 15.4; Stæhr and Sand-Jensen, 2007), variations in P_n were greater than 10-fold. The large daily variability in P_g is due to variations in cloud cover and resulting changes in sunlight (Fig. 15.4). Wind-induced changes in vertical mixing (Stæhr and Sand-Jensen, 2007) can also regulate fluctuations in ecosystem production. In shallow ecosystems, short-term increases in wind stress lead to higher rates of sediment resuspension, which reduces light penetration and thus P_g. Wind-induced resuspension may also reintroduce relatively labile organic matter into the water column (Demers et al., 1987), stimulating plankton community respiration and reducing rates of P_n (Dokulil, 1994). However, wind-induced resuspension can transport benthic diatoms into the water column, where they can access light and achieve higher rates of photosynthesis (Demers et al., 1987).

The exchange time of water parcels in estuarine ecosystems (i.e., the average time a given water parcel remains in the estuary) can also regulate the balance between photosynthesis and respiration by controlling the time that organic material may be processed within the system (Hopkinson and Vallino, 1995). Exchange time can vary within an estuary over seasonal and interannual time scales, particularly depending on changes in freshwater inputs (Hagy et al., 2000), tidal cycles, and offshore climatic variability. Modeling studies suggest that short exchange times would promote net autotrophy as dissolved inorganic nutrients are rapidly assimilated but particulate organic material is flushed from the system before being respired (Hopkinson and Vallino, 1995). In the LOICZ program, P_n rates and estuarine exchange times were computed for roughly 200 estuarine ecosystems (Crossland et al., 2005). These data indicate that P_n was negatively correlated with exchange time (Smith et al., 2005; Borges and Abril, 2011), with more variability in P_n with reduced exchange time. This suggests that longer exchange times increase net heterotrophy (or decrease net autotrophy) by increasing the amount of time that organic material can be respired within the ecosystem (Smith et al., 2005). Similarly, in the lower Patuxent River estuary, low exchange times are associated with elevated autotrophy (Fig. 15.6) because of high flushing of organic material out of the ecosystem (Vallino
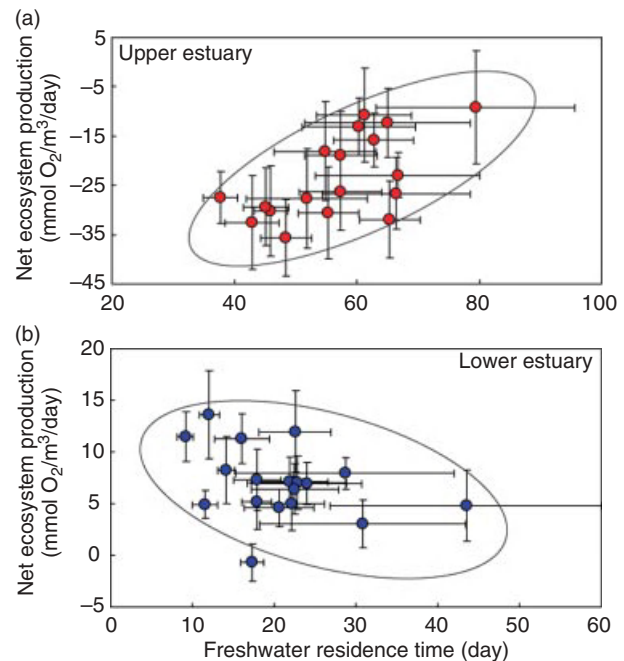
FIGURE 15.6 Relationships of freshwater residence time (FRT) with net ecosystem production (P_n = production-respiration) in two regions of the Patuxent River estuary (±SE; FRT from Hagy et al. (2000) and P_n data from Testa and Kemp (2008)). The data indicate that P_n is positively related to FRT in the upper estuary but that they are negatively correlated in the lower estuary.

et al., 2005) and stimulation of P_g via associated elevated nutrient input rates. In contrast, long exchange times lead to more autotrophic conditions in the turbid and shallow upper Patuxent River estuary, where reduced sediment input and enhanced stability of the water column allow elevated rates of P_g (Fig. 15.6).

15.4.6 Water Depth

The general depth dependence of metabolic balance (Odum, 1967; Alderman et al., 1995) regulates the relative dominance of primary producers and the relative contributions of benthic and pelagic rates to total ecosystem respiration. Because light levels reaching the sediment surface in shallow estuaries are often sufficient to support submerged vascular plants, P_n rates in these systems will likely be autotrophic because (i) such rooted plants are able to fix more CO_2 per unit nutrient input as their tissues have much higher ratios of C/N or C/P than microalgae and (ii) water column respiration rates tend to be low in clear-water environments (Ziegler and Benner, 1998). Thus, P_n shifts from net autotrophy to net heterotrophy with increases in depth
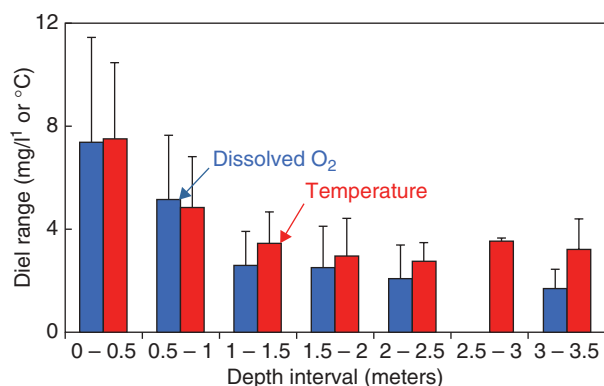
FIGURE 15.7 Average diel ranges (daily maximum–daily minimum) in water temperature and O_2 in 0.5-m depth categories in several Texas coastal bays during summer (Odum, 1967).

because water-column-integrated plankton respiration increases, while P_g does not change (Ryther, 1961; Wofsy, 1983) and benthic photosynthesis is inhibited by light limitation (Van de Bogert et al., 2007). In studies of the shallow turbid bays of the Texas coast, Odum (1967) noted an exponential decline in the daily excursions of O_2 (a measure of P_g) and temperature with depth (Fig. 15.7). This decline in variability indicated that large diel shifts in O_2 were representative of high metabolic rates found in shallow waters, where high O_2 excursions may be related to the presence of rooted autotrophs or to temperature stimulation of P_g and R (Fig. 15.7). Finally, it has been noted that depth controls the partitioning of ecosystem respiration between planktonic and benthic components, as planktonic processes are favored in deeper systems (Heip et al., 1995).

Depth interacts with nutrient status and habitat types to determine the dominant primary producers in an ecosystem and their effects on metabolic rates. Measuring individual components of an ecosystem using container incubations (e.g., Gazeau et al., 2005a) allows partitioning the contribution of various biotic units to P_n. Such an approach has been applied to studies focusing on the ecological role and metabolic contribution of seagrass and related submersed plants in shallow coastal environments. For example, seagrass growing in oligotrophic waters generally dominate shallow water P_n over an annual cycle in comparison to both adjacent areas without seagrass and other biotic components within the community. Seagrass beds also produce a clear metabolic signature in nutrient-poor, clear-water environments such as the Mediterranean Sea margins (Gazeau et al., 2005b). In nutrient-enriched environments,

such as the coastal Texas lagoons, seagrass contributions to P_a are often less important. In these lagoons, seagrass beds accounted for only approximately 30–40% of ecosystem P_a, with macroalgae (~30–45%), phytoplankton (~15–20%), and benthic microalgae (~10–35%) accounting for the remaining primary production (Kaldy et al., 2002). In addition, mesocosm experiments suggested that the relative contribution of seagrass to P_n tends to decline with high inputs of nutrients, because seagrass are either forced to compete with phytoplankton and epiphytic algae for nutrients or because water column nutrients cause algal and epiphyte shading that reduces light availability for seagrass growth.

15.5 ECOSYSTEM METABOLISM CASE STUDIES

Over the past several decades, certain coastal ecosystems have been sites of extensive integrated research focused on ecosystem metabolism and its relationship to key ecological, biogeochemical, and management factors. A subset of these sites represents an interesting combination of habitat types and physical settings, including a wide range of circulation patterns, depths, habitat types, dominant primary producers, and degrees of human perturbation. The following *case studies* of ecosystem metabolism provide an opportunity to explore a variety of metabolic patterns, while underscoring some important principles of coastal ecosystem ecology.

15.5.1 Tomales Bay

Tomales Bay is located at 38°N, 123°W in northern California and is a hydrographically simple estuary, with a linear basin of tectonic origin, modest rate of water exchange with the adjacent Pacific Ocean (Fig. 15.8c), and relatively shallow and uniform depths (Smith and Hollibaugh, 1997). The watershed has a Mediterranean climate (cool and wet winters, dry and hot summers) and a low population density, with grassland, forest, and chaparral ecosystems being dominant (Smith and Hollibaugh, 1997). Land clearing for agriculture (primarily potato farming) and logging in the latter half of the nineteenth century led to dramatically increased erosion and sediment transport to the bay through the first half of the twentieth century (Rooney and Smith, 1999). Otherwise, human impact on the system is low. Watershed carbon inputs are strongly related to interannual variations in winter rainfall and are primarily in the form of particles (Smith et al., 1996).
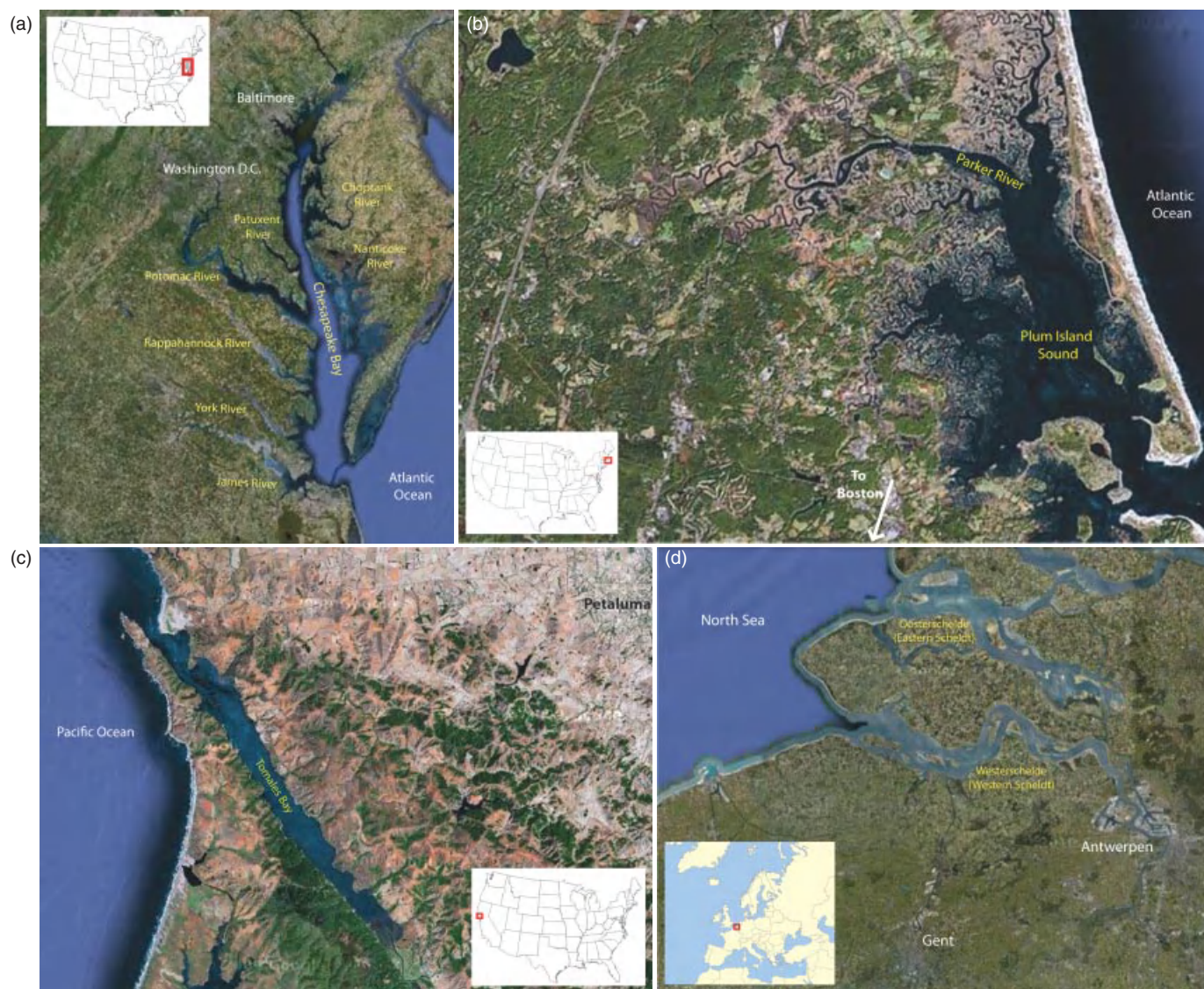
FIGURE 15.8 Maps of ecosystem metabolism case study estuaries and adjacent watersheds. *Source*: Areal maps from Google®.

(a)

(b)
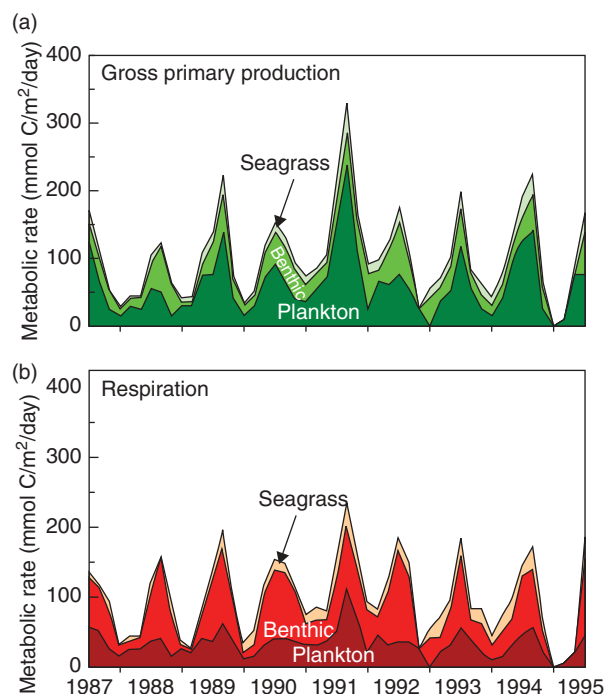
FIGURE 15.9 Time series of measurements of (a) P_g and (b) R for planktonic communities and both unvegetated and seagrass-dominated benthic communities in Tomales Bay, California, USA. *Source*: Data from Smith and Hollibaugh (1997).

Primary production in Tomales Bay is dominated by phytoplankton, but the seagrass *Zostera marina* contributes measurably to ecosystem metabolism (Fourqurean et al., 1997a). Throughout the bay, sediments without seagrass are colonized by a robust infaunal community and contribute substantially to ecosystem respiration (Fig. 15.9; Smith and Hollibaugh, 1997). Additional site characteristics are listed in Table 15.1. Tomales Bay was the site of extensive studies concerning metabolic rates of various community types over the course of a decade as part of the United States National Science Foundation's Land Margin Ecosystem Research (LMER) program. Among other accomplishments, diverse studies at Tomales Bay provided insights into the external drivers of the bay's metabolism and accomplished perhaps the first analysis of interannual variations in metabolism by applying a systematic methodology using biogeochemical budgets (Section 15.3.5). This study also quantified relative contributions of particular ecosystem components to whole-ecosystem metabolism (Dollar et al., 1991; Smith and Hollibaugh, 1997).

Partitioning of the metabolism of distinct habitats in Tomales Bay allowed an understanding of the contribution of the various habitats to whole-ecosystem

production. Seasonal metabolic cycles followed the seasonal temperature cycle, with net heterotrophy dominating during the July to September period (Smith and Hollibaugh, 1997). The plankton and heterotrophic benthic communities dominated Tomales Bay metabolism (Fig. 15.9). Although plankton dominated P_g in Tomales Bay, benthic communities dominated respiration, and net system heterotrophy indicated that a carbon source aside from internal phytoplankton production must exist (Fig. 15.9). A subsequent analysis of organic carbon imports indicated that watershed inputs (via stream flow) and tidal influxes of labile organic material from the Pacific Ocean, associated with seasonal variations in upwelling, contributed about equally to this additional carbon (Smith and Hollibaugh, 1997).

This study was one of the first to emphasize and quantitatively support the idea that ecosystem metabolism for small estuaries adjacent to regions of coastal upwelling are often strongly influenced by import of marine detrital organic matter and upwelling events appear to be better correlated to P_n than to other carbon sources, at least over part of the time series (Fig. 15.10; Smith and Hollibaugh, 1997).

15.5.2 Parker River-Plum Island Sound

Plum Island Sound is located at $43°N$, $-71°W$ on the northeast coast of Massachusetts and is fed by three rivers along its 24 km length, including the Parker, Ipswich, and Rowley (Fig. 15.8b). The suburban watershed is within the Boston Metropolitan Area, with about 40% of the area classified as "urban," and the watershed retains large areas of forest, wetlands, and ponds. A bar-built estuary, Plum Island Sound exchanges with the Gulf of Maine through a single inlet near its southern terminus. A small connection between Plum Island Sound and the Merrimack River to the north creates a net residual circulation from the ocean to the Merrimack (Zhao et al., 2010). The sound and river system are shallow (mean depth ~2 m) and vertically well-mixed (Hopkinson et al., 1999). The estuary is fringed by tidal salt marshes dominated by *Spartina alterniflora* and *S. patens* (Hopkinson et al., 1999; Fig. 15.8b). The estuary is approximately 25 km long, with a tidal river in the upper half (wetland/water area = 5 : 1) and a broad shallow bay in the lower half (wetland/water area ≈1 : 1). Although the population density in the watershed is moderate, a mostly intact riverine riparian zone with extensive wetlands helps minimize inorganic nutrient levels and eutrophication in the system. In fact, dissolved organic nitrogen concentrations exceed inorganic N levels (Williams et al., 2004). The temperate climate in this region results in

TABLE 15.1 Coastal systems that are highlighted as case studies in Section 15.5

System Name	Estuary Type	Salinity	Mean Depth, m	Watershed Population	Nutrient and Organic Matter Load Source	Population density (people/km^2)
Chesapeake Bay	Coastal plain	0–30	6.5	~16,000,000	Agricultural runoff, wastewater, atmospheric	100
Plum Island Sound	Coastal plain, bar-built	0–32	1.4 (head) 4.7 (mouth)	~150,000	Watershed runoff, some wastewater	250
The Scheldt	Well mixed	0.5–28	7 (Gent) 14 (mouth)	~10,000,000	Wastewater	450
Tomales Bay	Lagoon	20–35	3	~11,000	Coastal upwelling, watershed runoff	20
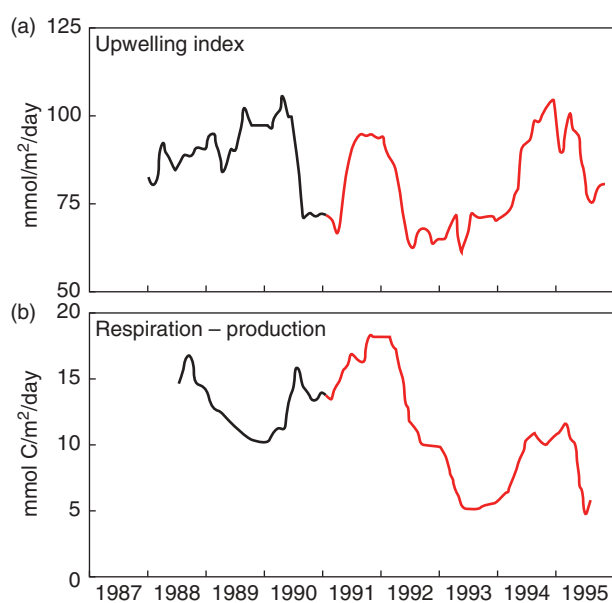
FIGURE 15.10 Time series of (a) 1-year moving averages for an upwelling index on the Pacific coast and (b) net ecosystem respiration ($R - P$) in the Tomales Bay, California, USA. Data from Smith and Hollibaugh (1997) and reprinted with permission. The correlation between the upwelling index and $R - P$ from 1991–1996 (and lack of correlation between watershed POC and $R - P$ over the same time period) suggests that upwelling-derived organic inputs fuel net heterotrophy in this ecosystem.

cold winters and mild summers, with seasonal peaks in discharge occurring during spring, as snow melts and evapotranspiration is low. Plum Island Sound and its associated estuaries were extensively studied via the United States National Science Foundation's long-term ecological research (PIE-LTER) program. This program investigated the long-term response of watershed and estuarine ecosystems at the land–sea interface to changes in climate, land use, and sea level.

Most studies of the metabolism of Plum Island Sound focused on spatial variations along the salinity gradient of the Parker River-Plum Island Sound (Fig. 15.11; Alderman et al., 1995; Hopkinson et al., 1999). In this well-mixed linear system, free-water diurnal measures of metabolism were developed for the entire length of the estuary (Vallino et al., 2005). Continuous measures of dissolved O_2 and/or TCO_2 within a 45-min period at dawn and dusk along the entire length of the estuary enable continuous estimates of P_g, R_n, and P_n, once corrected for air–sea exchange (F_{aw}). Despite high turbidity in the upper reaches of the Parker River, P_g rates in this region exceed those of more seaward waters (Fig. 15.11; Alderman et al., 1995; Vallino et al., 2005). Such high P_g, despite high turbidity, is mostly due to phytoplankton blooms during periods of low river runoff and consequently long water exchange times. Elevated per-cell chlorophyll a levels in the region (phytoplankton increase chlorophyll a to harvest more light in turbid conditions) combined with salinity-enhanced rates of benthic nutrient flux and shallow depths promote these high rates of production (Alderman et al., 1995; Hopkinson et al., 1999). Net autotrophy in these low-salinity regions during summer gives way to net heterotrophy in midregions of the estuary (Alderman et al., 1995; Vallino et al., 2005), which is due to down-estuary transport of carbon into this region (from watershed and low-salinity region) and import of labile organic matter from the extensive marshes flanking the estuary. Although pelagic respiration is relatively constant along the estuarine salinity gradient, benthic respiration is much higher in the middle of the Parker River than sites upstream and downstream (Fig. 15.11; Hopkinson et al., 1999), comprising nearly all ecosystem respiration at the site. Although the midriver site may have received exceptional amounts of organic carbon from the adjacent marshes, this site was also
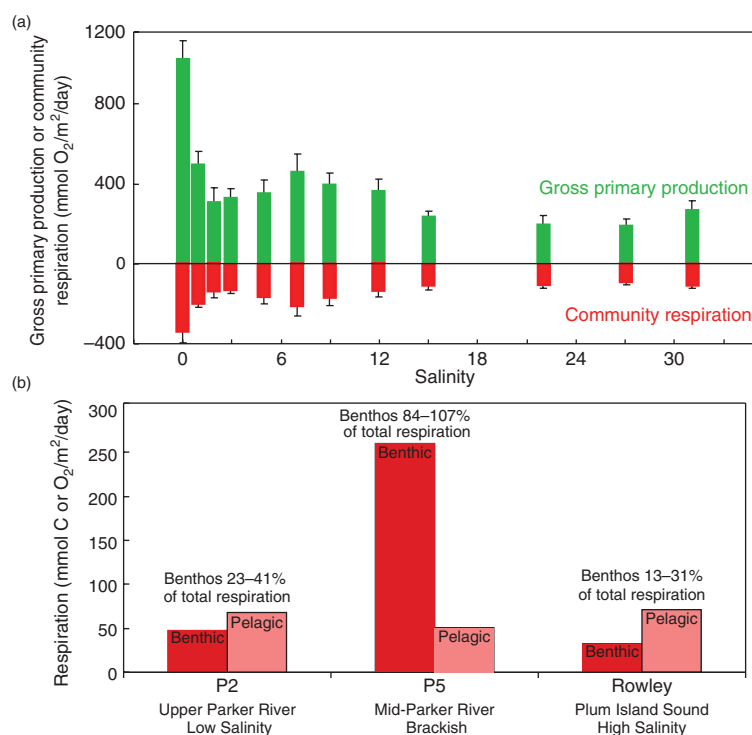
FIGURE 15.11 (a) Model-estimated instantaneous gross primary production (P_g) and community respiration (R) at noon along the estuarine transect of the Parker River-Plum Island Sound estuarine system in northeastern Massachusetts, USA. Model data from Vallino et al. (2005). (b) Contributions of benthic and pelagic metabolism at three stations along the salinity gradient of the Parker River-Plum Island Sound estuarine system. The lower value in the range of benthic percentage contribution to total respiration is based on the fraction of total ecosystem metabolism (measured via nighttime water column O_2 consumption) that is contributed by benthic uptake of TCO_2 (converted to O_2 units using an RQ = 1). The upper range is the fraction of benthic respiration that contributes to benthic + water column respiration (measured in BOD bottles). *Source*: Data from Hopkinson et al. (1999).

dominated by the soft shelled clam, *Mya arenaria*, which likely contributed significantly to the benthic respiration rates (Hopkinson et al., 1999).

Continuing studies at Plum Island Sound are focused on modeling the long-term effects of climate change and sea level rise on these processes. For example, one goal is to investigate the possibility that large increases in river discharge will shift the productivity maxima seaward because of increases in turbidity and respiration driven by organic matter imported from the surrounding watershed and marshes (Hopkinson and Vallino, 1995).

15.5.3 Chesapeake Bay System

Chesapeake Bay is located at 38 °N, 76 °W in the middle of Atlantic coast of the United States and is fed by several large rivers, most notably the Susquehanna River (Fig. 15.8a), which supplies more than half of the freshwater flow (Kemp et al., 2005). The temperate climate in this region results in cold winters and warm summers, with seasonal peaks in discharge occurring

during spring, as snow melts and precipitation is high. A partially stratified estuary, Chesapeake Bay is characterized by two-layer circulation, including a seaward-flowing surface current and a landward-flowing bottom current. The bottom current generally moves through a deep, central channel, which is flanked by extensive shallow areas such that approximately 75% of the bay surface area is shallower than 10 m (Kemp et al., 2005). Relatively large freshwater inputs drive a strong longitudinal salinity gradient and induce stratification in the deep, central parts of the bay, which prevents mixing of deeper waters with surface water and the atmosphere. Chesapeake Bay exchanges with the Atlantic Ocean at its southern terminus (Fig. 15.8a). Although the population density in the watershed is moderate, the dominance of agriculture throughout much of the watershed and large population centers (Baltimore and Washington, D.C.) adjacent to Chesapeake Bay result in large nutrient loads to the estuary, leading to elevated nutrient levels and extensive eutrophication in the system (Kemp

et al., 2005). Eutrophication in this estuary has been reinforced by the loss of once-extensive sediment-stabilizing seagrass beds and water-filtering oyster reefs throughout the bay's shallow flats, as well as a large watershed to water volume ratio (Table 15.1). Chesapeake Bay and its tributary estuaries were extensively studied for over seven decades, revealing many key processes and external drivers in the bay's ecosystem.

One of the more pressing ecological concerns over recent decades in Chesapeake Bay and its tributaries is the seasonal development of low-O_2 waters in deeper sections of the central channel (Hagy et al., 2004). *Hypoxia* (O_2 <20%−30% saturation, 2 mg/l, or 62.5 µM) and *anoxia* (0% saturation or <0.1 mg/l, 6.25 µM) are important consequences of human activities and eutrophication of estuaries and bays worldwide. Eutrophication-induced hypoxia occurs in stratified coastal systems through nutrient stimulation of surface layer phytoplankton production and sinking, which in turn leads to stimulation of bottom layer respiration (Testa et al., 2008; Rabalais and Gilbert, 2009). These metabolic processes provide a link between nutrient inputs and seasonal depletion of bottom water O_2 (Kemp et al., 2009). Hence, coastal hypoxia is often associated with increases in ecosystem production and respiration, with elevated net autotrophy in surface layers and higher net heterotrophy in underlying waters (Kemp et al., 2009). Considering that the organic matter produced in surface waters supports much of the benthic and plankton respiration, the coupling of surface production and bottom respiration is a key driver of bottom water O_2 depletion in Chesapeake Bay and many similar systems (Rowe, 2001; Conley et al., 2009).

In Chesapeake Bay, oxygen and carbon budgets, as well as seasonal cycles of ecosystem metabolism, were used to infer sources of organic material and sinks of oxygen that drive hypoxia (Fig. 15.12; Kemp et al., 1997). Such budgets support two following primary conclusions: (i) planktonic production and respiration dominate bay C budgets and (ii) surface waters (and the whole bay) are net autotrophic (Kemp et al., 1997). Further investigations of the spatial and seasonal variations in planktonic metabolic balance indicate several key features of planktonic contributions to particle sinking and bottom layer respiration. Rates of planktonic P_g and R are lowest in the upper bay, where high flushing and elevated rates of allochthonous organic matter inputs from the Susquehanna River cause light limitation of P_g (Fig. 15.12). This region of the estuary is also net heterotrophic in all months, as imported organic matter fuels respiration over production (Fig. 15.12; Smith and Kemp, 1995). In the middle and lower bay, elevated light availability allows for seasonal peaks in P_g and R, coincident with summer peaks in photosynthetically active radiation (PAR) and water temperature (Fig. 15.12). However, P_g increases more rapidly than R during the March to May period, resulting in spring peaks in P_g that correspond to the spring diatom bloom in the Chesapeake Bay (Fig. 15.12, green areas). A second peak in P_n occurs in late summer, after a approximately 2-month period of net heterotrophy during the crash of the spring diatom bloom and transition into blooms of smaller dinoflagellates during July and August (Fig. 15.12). The net result of these spatial/temporal dynamics is that spring and summer periods of net autotrophy in the middle and lower estuary generate the excess carbon that can fuel bottom water O_2 consumption (Smith and Kemp, 1995). Similar patterns exist in the adjacent Patuxent River estuary, where biogeochemical budget computations (Chapter 17) suggest a spring peak in surface water autotrophy and an extended period of net heterotrophy in bottom waters (Testa and Kemp, 2008).

In stratified estuaries such as Chesapeake Bay and the Patuxent estuary, a ''metabolic separation'' exists in which watershed nutrient inputs in the surface layer stimulate excess P_n (i.e., organic matter production), some of which sinks to bottom layers where net respiration (e.g., organic matter consumption) prevails. Consequently, surface layer P_n in these estuaries correlates strongly with the sinking of organic material and subsequent bottom layer respiration. In the Patuxent River, surface layer P_n peaks in spring (Testa and Kemp, 2008) when nutrient inputs are high and temperature (and thus respiration) is relatively low; this is the period of the conventional ''spring bloom'' in temperate estuaries. Bottom layer respiration (water column and sediments) lags behind the period of peak surface layer P_n, as respiration is delayed until June−August, when temperature peaks. Although surface layer P_n declines over this summer period as respiration increases, surface and bottom layer P_n are proportional to each other over annual time scales (Testa and Kemp, 2008).

In the main-stem Chesapeake Bay, P_n in the surface layer correlates with measurements of sinking POC captured in sediment traps (Fig. 15.13). Thus, both the amount of POC sinking to bottom waters and the resulting respiration rates appear to be proportional to excess C production in surface waters (Fig. 15.13). Similarly, P_n measured in mesocosms of the Narragansett Bay correlated strongly with the production of flocculent organic material. Both P_n and
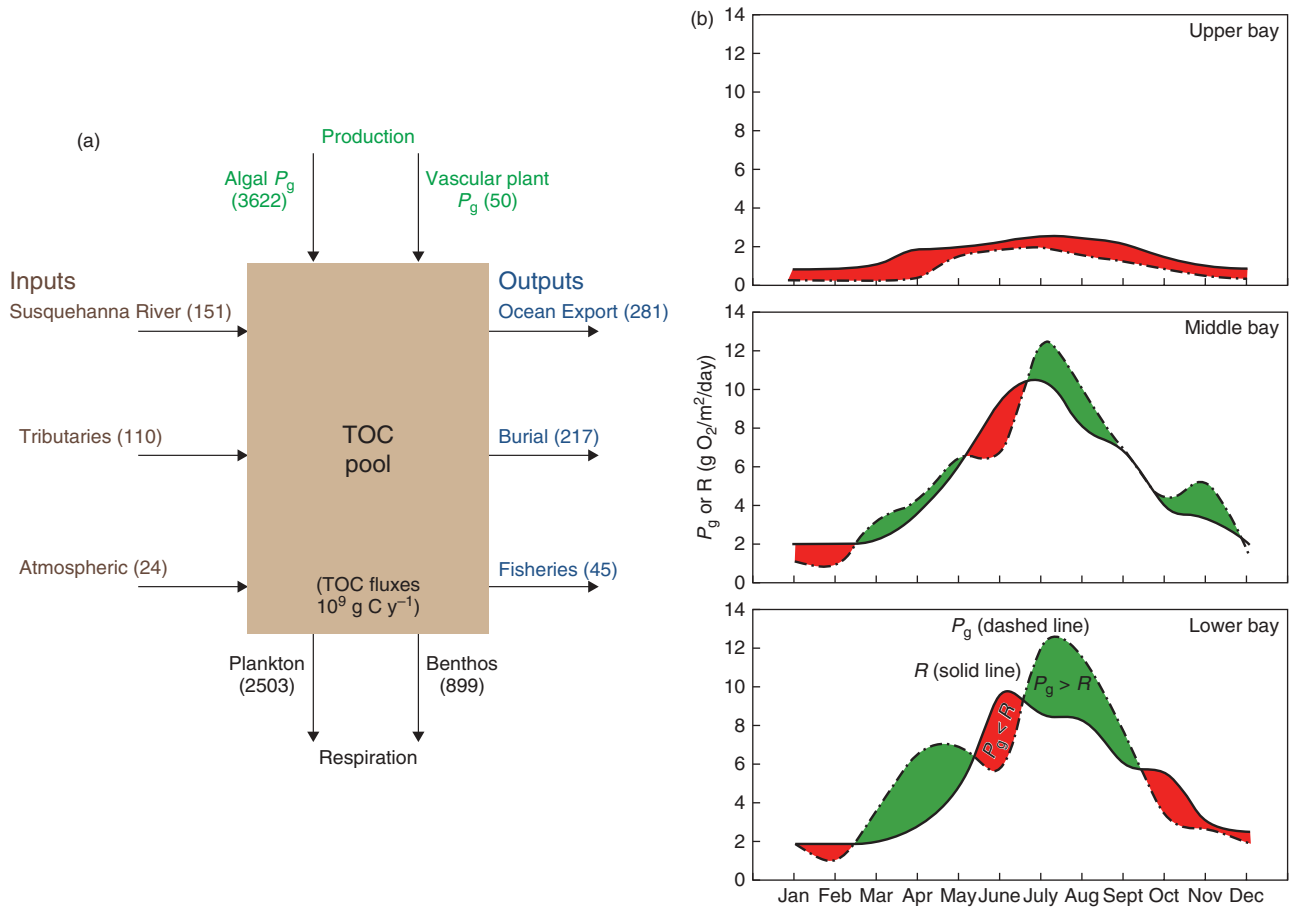
FIGURE 15.12 (a) Steady state organic carbon budget for the main stem of the Chesapeake Bay, including biogeochemical rates and physical transports (Data from Kemp et al., 1997). (b) Seasonal distribution of P_g and R for the main stem of the Chesapeake Bay in the upper, middle, and lower regions of the Bay. The upper estuary is net heterotrophic, while the middle and lower Bay are progressively net autotrophic, with March to May (the spring diatom bloom) and July to September (picoplankton dominated) periods dominating the net production.

flocculent production were stimulated by inorganic nitrogen additions (Fig. 15.13). Additional inputs of dissolved silica (DSi) further enhanced the flocculent material production per unit P_n. This occurred because diatoms tend to rapidly take up nutrients and their large cells lead to rapid organic matter accumulation, which is much like their growth in natural estuaries during the spring bloom (Fig. 15.13). These examples illustrate how elevated nutrient inputs to coastal systems around the globe stimulates the production and subsequent consumption of organic matter, causing O_2 deficiencies in the bottom waters of the Chesapeake Bay and many other ecosystems (Kemp et al., 2009).

15.5.4 Scheldt Estuary

The Scheldt estuary is located at $51\,°$N, $4\,°$W in northern Europe, and its 19,500 km^2 watershed covers parts of France, Belgium, and The Netherlands (Fig. 15.8d; Gazeau et al., 2005c). The Scheldt and its delta include eastern and western sections (Oosterschelde and Westerschelde). The river Scheldt contributes the majority of freshwater to the estuary, which empties into, and exchanges with, the southern part of the North Sea (Fig. 15.8d). The temperate climate in this region results in cold winters and mild summers, with seasonal peaks in discharge occurring during spring. Because tidal currents are strong, the estuary is well-mixed, with axial salinity ranging from 0.5 to 28. The mean depth of the estuary varies along its axis, from 7 m near Ghent and 14 m near the mouth. The watershed includes the Belgian cities of Antwerp and Ghent, and the total watershed population approaches nearly 10,000,000 people. As a result of high human population densities (450 people/km^2), the Scheldt estuary is one of the most polluted rivers in Europe, receiving large quantities of nutrients and organic matter from agriculture and wastewater sources (Gazeau et al., 2005c; Soetaert et al., 2006). Owing to the high level of anthropogenic disturbance in its watershed, the Scheldt estuary provides a useful example of the effects of pollution on metabolism.

Although tidal flats flank the main estuary channel in the lower reaches of the estuary, the Scheldt's metabolism is dominated by phytoplankton and bacteria along most of its axis. Despite the fact that the Scheldt is highly turbid, net phytoplankton production occurs along the length of the estuarine axis and peaks occur in low-salinity regions of the estuary and near the seaward terminus (Fig. 15.14; Gazeau et al., 2005c). Interestingly, net phytoplankton production has been found to be possible in other well-mixed, highly turbid estuaries, where nutrient limitation is absent (DIN >200 μM, DIP >5 μM) and water depth is shallow enough to allow phytoplankton to access light for sufficient amounts of time.

However, owing to high inputs of relatively labile organic matter from wastewater treatments plants (Soetaert et al., 2006) and watershed runoff, bacterial respiration is high, leading to highly heterotrophic net ecosystem metabolism (Fig. 15.14; Gazeau et al., 2005c). Net respiration peaks in low-salinity water, where organic materials accumulate because of close proximity to wastewater discharges and physical forces (Fig. 15.14). Consequently, despite extremely high levels of inorganic nutrient inputs to the Scheldt, the system is net heterotrophic, because of high levels of respiration of imported organic matter combined with light limitation of algal growth (Kromkamp and Van Engeland, 2010). Thus, this estuary does not fit the relationship between P_n and the ratio of DIN/TOC (total organic carbon) that characterizes many temperate estuaries that are primarily nutrient limited (Fig. 15.5).

In addition to high organic matter inputs, extensive nutrient inputs to the Scheldt may have reduced primary production and promoted heterotrophy. Extremely high wastewater NH_4^+ inputs causes extremely high NH_4^+ concentrations in the freshwater region of the estuary (>900 μM; Fig. 15.15). At these levels, NH_4^+ is toxic to algae, leading to the inhibition of photosynthesis and the resultant low levels of chlorophyll a in the estuary (Fig. 15.15; Cox et al., 2009). As management actions reduced NH_4^+ concentrations in the Scheldt over the past two decades, chlorophyll a concentrations tripled (Soetaert et al., 2006; Cox et al., 2009). Another consequence of the high NH_4^+ is the stimulation of nitrification under oxic conditions. Nitrification-based O_2 demand caused hypoxia throughout much of the inner Scheldt estuary, which may have further inhibited photosynthesis in the 1960–1990 period (Soetaert et al., 2006). Nitrification, however, is a chemoautotrophic process that generates organic material; thus unlike many estuaries, high NH_4^+ concentrations support nitrification at sufficient rates to contribute to carbon production (just as P_g) in the Scheldt (Fig. 15.15; Gazeau et al., 2005c). It is unclear how the balance between NH_4^+-driven reductions in photosynthesis and NH_4^+-driven nitrification-based carbon production has changed P_n over the past 50 years. Considering the tendency for net heterotrophy in this system in all seasons, potential shifts toward elevated autotrophy over time would surely have been overwhelmed by high respiration rates (Fig. 15.15).
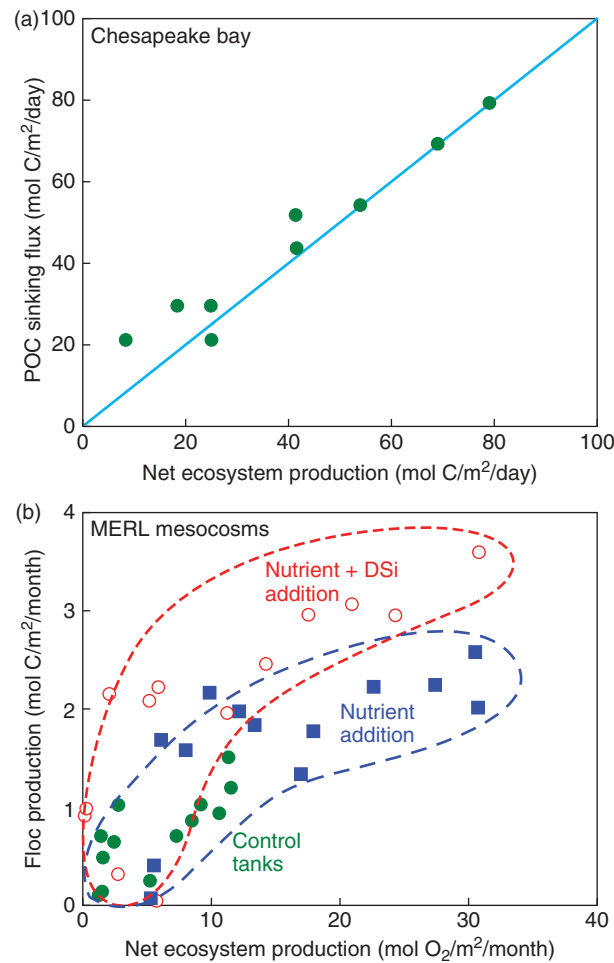
FIGURE 15.13 Correlations between net ecosystem production and indexes of organic particle formation in (a) the Chesapeake Bay, where net plankton production is highly correlated to sediment trap collection rates (Boynton and Kemp, unpublished data) and (b) MERL mesocosms, where net ecosystem production is highly correlated to the accumulation of organic flocs (Oviatt et al., 1993).

15.6 CROSS-ECOSYSTEM COMPARISONS

Over the past two decades, a few efforts have examined the state, dynamics and drivers of ecosystem metabolism across many different ecosystems. In this section, we review a few examples of cross-system comparisons of coastal ecosystem metabolism and the lessons learned from the efforts.

15.6.1 Trophic State and Dominant Controls

Under the auspices of the Land-Ocean Interactions in the Coastal Zone program (LOICZ,

http://www.loicz.org/, a project of the International Geosphere-Biosphere Program, IGBP), a major scientific effort was to compile carbon, nitrogen, and phosphorus data for coastal systems around the world and apply the data to construct carbon and nutrient budget models using a consistent and relatively simple methodology (http://nest.su.se/mnode/). Among other system properties, these analyses produced estimates of net ecosystem production, based on the net nonconservative production of inorganic phosphorus (Smith et al., 2005; Section 15.3.4). As a result, comparable estimates of P_n were made for approximately 200 ecosystems across the globe, and analyses of these estimates provided key insights into the global trophic tendency of coastal systems, as well as
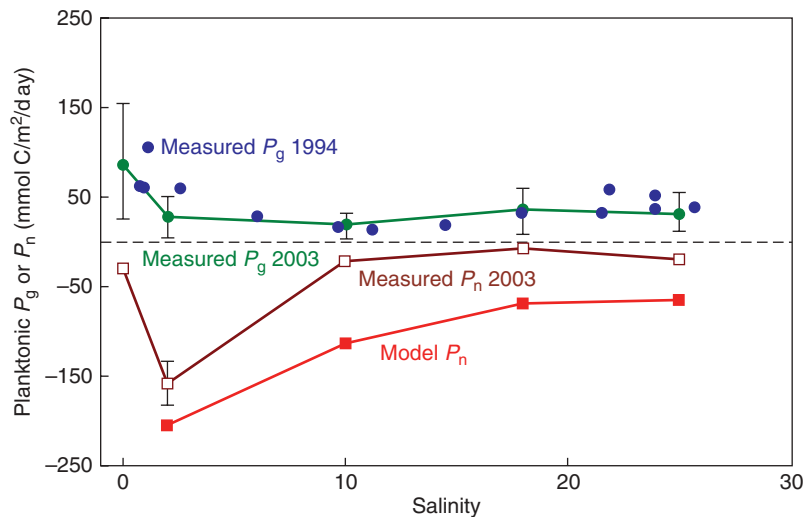
FIGURE 15.14   Distribution of P_g and P_n (of plankton community) along the salinity gradient of the Scheldt estuary. Open, maroon squares are measured P_n in 2003 (Gazeau et al., 2005c) and are compared to modeled P_n rates (filled, red squares) from Soetaert and Herman (1995). Blue circles are the measured P_g rates from Kromkamp and Peene (1995) and green circles are the measured P_g rates from 2003 (Gazeau et al., 2005c). *Source*: Figure adapted from Gazeau et al. (2005c).

insight into patterns and controls of ecosystem metabolism.

The system-wide synthesis of LOICZ P_n rates for approximately 200 coastal ecosystems across the globe (Smith et al., 2005) revealed that the net metabolism of these estuaries and bays tends to be close to zero and that slightly more systems were autotrophic than heterotrophic (Fig. 15.16). This tendency toward net autotrophic ecosystems may reflect the rapid global expansion of coastal eutrophication, driven primarily by inorganic nutrients from runoff of agricultural fertilizers and from secondary-treated sewage, which would favor primary production over respiration. Despite the impressive number of systems analyzed in LOICZ, the sample size is still too small to infer generalizations about the tendency for estuaries to be net autotrophic or heterotrophic on a global scale. The fact that other studies have found estuaries to be generally heterotrophic (Borges and Abril, 2011) suggests that the metabolic state of any particular estuary is specific not only to its watershed, climate, and bathymetry but also to the particular season and year in which the measurements were made, with their characteristic human impact and year-specific climatic regime. Although many coastal systems across the world are receiving large inputs of inorganic nutrients, the large number of systems characterized by heterotrophic metabolism suggests that (i) organic matter inputs from surrounding watersheds and wetlands tends

to fuel high respiration rates and that (ii) characteristically high turbidity in estuaries often restricts photosynthesis. For example, a recent comparative analysis of coastal ecosystem metabolism (Caffrey, 2004) suggested a predominance of heterotrophic systems, most of which were flanked by mangrove or marsh ecosystems, which tend to export large amounts of relatively labile organic matter.

15.6.2 Eutrophication Effects on Metabolism

As discussed in Section 15.4, ecosystem metabolism has been shown to respond strongly to a wide range of anthropogenic disturbances to coastal systems including increases in inputs of toxic contaminants, suspended sediments, inorganic nutrients, and labile organic matter. In this chapter, we have emphasized how measurements and calculations of coastal ecosystem net production (P_n) are useful for distinguishing the relative importance of external inputs of inorganic nutrients versus labile organic matter. The former tends to increase P_n, while the latter drives P_n negative. In several important papers in the 1990s, budgets (Smith and Hollibaugh, 1993) and data syntheses (Heip et al., 1995) were used to understand the trophic state of the coastal zone. It was suggested that the coastal zone was net heterotrophic, because of high inputs of organic matter from adjacent watersheds, marshes, and human population centers. These analyses emphasized that estuaries, despite being net heterotrophic, were also highly productive because
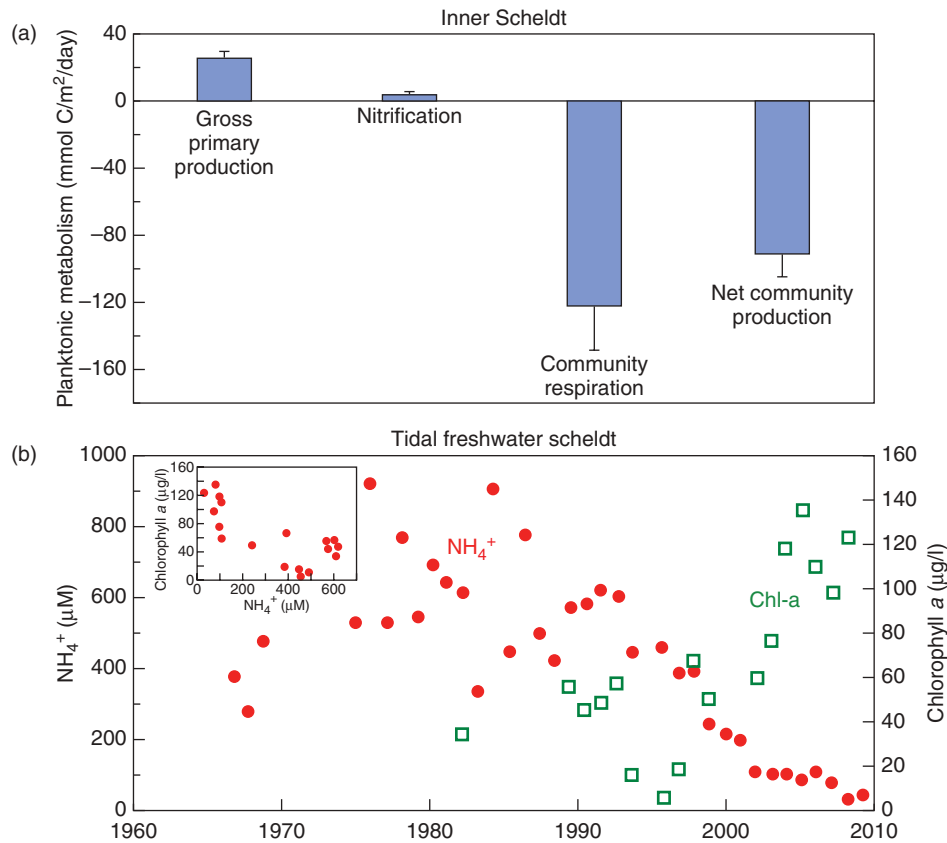
FIGURE 15.15 (a) Annual mean components of metabolism in the inner Scheldt estuary (data from Gazeau et al., 2005c). The data indicate a high level of community respiration, because of high organic matter inputs rates to this system and also a nonnegligible contribution of nitrification (a chemoautotrophic process) to organic carbon production in the estuary. (b) Time series of NH_4^+ and chlorophyll a concentrations averaged over the tidal freshwater region of the Scheldt estuary from 1967 to 2008 (inset is correlation between the annual data, which are from Cox et al. (2009) and sources cited within). High NH_4^+ concentrations prevailed through the mid-1990s, until management actions dramatically reduced NH_4^+ concentrations after 2000.

primary production tends to be stimulated by nutrients regenerated from respiration of imported organic matter (Smith and Hollibaugh, 1993; Heath, 1995; Heip et al., 1995). This initial perception was likely influenced by the types of systems included in this analysis, which included few deep, eutrophic estuaries (Fig. 15.17). Organic matter-enriched watersheds are those impacted by human perturbation, and some are naturally impacted by high organic matter loads and display a negative relationship between P_g and P_n. Systems with increasingly negative P_n (higher respiration) are associated with higher nutrient remineralization rates to fuel elevated P_g (Smith and Hollibaugh, 1993). This is also true for the shallow, turbid systems analyzed by Caffrey (2004), many of which are flanked by tidal marshes ("Shallow, marsh-flanked") or other ecosystems that tend to export organic material. For eutrophic systems with elevated nutrient inputs and relatively high light availability, P_n is positively related to P_g because nutrient loads stimulate P_g. A 1000-year simulation of organic inputs and metabolism for the coastal zone (blue circle) includes low rates but follows the pattern for marsh-flanked ecosystems (Ver et al., 1994). Because forests tend to conserve inorganic nutrients, but often export DOC and POC from plant debris and soil materials, drainage from forested or disturbed watersheds would tend to support moderately heterotrophic estuaries (Fig. 15.17). Estuarine waters that are surrounded by tidal marshes and mangroves tend to be even more heterotrophic despite high P_g, given the high nutrient regeneration from substantial labile DOC and POC exports from those wetlands (Fig. 15.17). Conversely, in plankton-dominated estuaries receiving high levels of inorganic nutrients but moderate levels of organic matter, nutrient-driven increases in P_g would tend to cause elevated P_n (Fig. 15.17). As human populations and impacts of
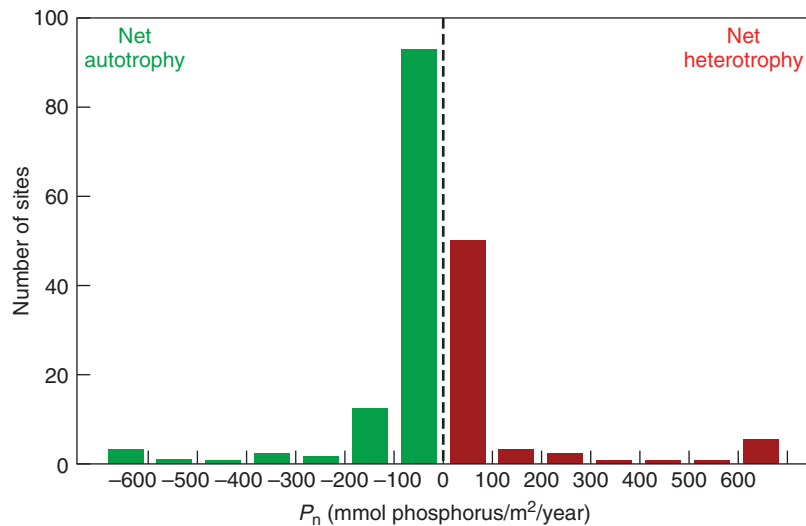
FIGURE 15.16 Frequency distribution of P_n derived from computations of the net nonconservative production rates of dissolved inorganic phosphorus from budget estimates for coastal systems around the world. Rates are from Smith et al. (2005) based on the LOICZ biogeochemical budget model analysis.
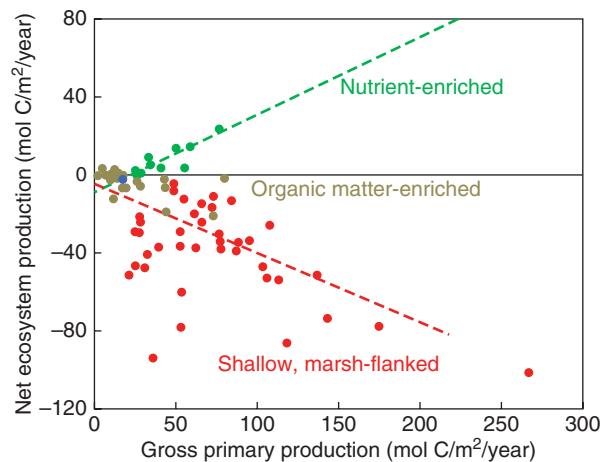
FIGURE 15.17 Relationships between net ecosystem production (P_n) and gross primary production (P_g) for ecosystems under various land use and anthropogenic impacts. *Source*: Data from reported values in the literature (Nixon and Pilson, 1984; Oviatt et al., 1986; Smith and Hollibaugh, 1993; Ver et al., 1994; Kemp et al., 1997; Caffrey, 2004; and Testa, unpublished).

land use continue to grow and develop, the future trajectory of metabolic balance in coastal ecosystems is unclear.

As just mentioned, a number of publications have linked elevated P_n to increases in inorganic nutrient inputs (Oviatt et al., 1986; Testa et al., 2008). Such increases are expected for relatively clear-water systems that are generally nutrient limited. The consequences of elevated P_n in the face of global increases in anthropogenic nutrient inputs include elevated carbon fluxes from coastal surface waters to adjacent ecosystems. A primary sink for excess carbon production in surface waters is the underlying bottom waters, and eutrophication has been linked to increasing bottom water and sediment respiration rates, and associated depletion of O_2 (Kemp et al., 2009). Thus, elevated nutrient inputs not only increases surface water P_n but also enhances metabolic processing within the whole ecosystem, as fresh organic material is respired at higher rates.

15.6.3 Coastal Ecosystems and Global Carbon Balance

Several ongoing research efforts have used measurements and/or computations of ecosystem metabolism to examine the contribution of coastal ecosystems to the global balance of carbon dioxide. Such analyses quantify the net fluxes of CO_2, the extent to which these systems are net sources or sinks, and how their metabolism might influence atmospheric CO_2 and associated climatic changes. It is inherently difficult to make these calculations for many reasons including (i) data must be dependable and cover adequate temporal and spatial scales, (ii) errors associated with extrapolating these measurements to large scales are uncertain but can be substantial, (iii) the wide diversity of coastal systems and associated metabolic characteristics makes generalizations especially difficult, (iv) physical transport terms in CO_2 and O_2 budgets are often uncertain and much larger than the metabolic terms, and (v) the lability

of organic material in these budgets is rarely quantified. Despite these difficulties, various estimates of metabolic balances in coastal zones have provided interesting perspectives on coastal contributions to global CO_2 dynamics (Crossland et al., 1991; Smith and Hollibaugh, 1993; Duarte et al., 2005; Borges and Abril, 2011).

Early budgets of the global CO_2 balance suggested that the net metabolism of the world's oceans represents a major sink for atmospheric CO_2 (Woodwell and Pecan, 1973), and subsequent measurements suggested that vertical sinking of surface water net production of organic matter could by an important mechanism drive this sink. Subsequent analyses using bottle incubations (Duarte and Augusti, 1998; Williams, 1998) and ocean-scale distributions of surface CO_2 and O_2 partial pressures (Najjar and Keeling, 2000; Takahashi et al., 2002; Cai et al., 2006) have revealed strong seasonal and regional variations in oceanic P_n, suggesting a variable trophic state for the open ocean. Regardless of the magnitude and sign of global ocean P_n, computations of integrated net metabolic rates for particular coastal biomes provide a perspective on their potential contributions to CO_2 balance in the global ocean or in specific ocean basins. For example, estimates for coral reef metabolism indicated that their global gross production amounts to approximately 2% of oceanic net production; however, P_n for coral reefs comprises approximately 0.05% of net biological CO_2 influx in the global ocean (Crossland et al., 1991). More importantly, as calcification in coral reefs generates CO_2, the biological *and* geochemical processes on coral reefs generate a net efflux of CO_2 to the atmosphere on the order of $0.02-0.08$ Gt C y^{-1} (Ware et al., 1991). The combined P_n for all shallow vegetated habitats in the coastal ocean (e.g., mangroves, salt marshes, seagrass, macroalgae) is estimated to exceed that of the pelagic ocean, and the computed carbon burial in these vegetated biomes approximates that estimated for the entire open ocean (Duarte et al., 2005). This analysis suggests that these shallow vegetated habitats play a critical role in maintaining the oceanic sink for atmospheric CO_2. However, C burial in vegetated coastal sediments has been and is likely to continue to decrease substantially in the future in conjunction with global warming, sea-level rise, and continued reclamation of wetlands (Hopkinson et al., 2012).

In contrast, early budgets comparing land−sea carbon transport to carbon burial suggest that the coastal zone is a net source of CO_2 to the atmosphere (Smith and Hollibaugh, 1993). This conclusion is supported by recent meta-analyses (Borges and Abril, 2011). However, recent studies applying air−sea gas exchange measurements of P_n have concluded that net heterotrophy in estuaries and coastal bays (i.e., the ''narrow oceanic fringe'') is counterbalanced by net autotrophy in continental shelf ecosystems, thereby preserving the ocean's status as a net sink for CO_2 (Borges and Abril, 2011). Recent studies suggest that continental shelves at mid to high latitudes are net sinks for atmospheric CO_2, but a net source in lower latitudes, where higher temperatures enhance respiration of terrestrial inputs of organic material in the tropics (Cai et al., 2006).

15.7 METABOLIC RESPONSES TO CLIMATE CHANGE AND VARIABILITY

Climatic change and variability are expected to alter both respiration and primary production of aquatic ecosystems through a variety of mechanisms and pathways. Although it is widely expected that the climate of Earth system will change over the next century, the anticipated magnitude and nature of these changes varies widely depending on geographic location and modeling approach. Most model predictions of global climate change, however, predict regional increases in ambient temperature, shifts in precipitation and storm frequency (Mulholland et al., 1998, Chapter 20), and increased acidity of the ocean (Hoegh-Guldberg et al., 2007).

These changes in watershed land use and climatic and biogeochemical conditions are all likely to alter regional and global rates and balances between P and R (Hopkinson and Vallino, 1995). Elevated precipitation would tend to increase ecosystem production in temperate, deeper estuaries due to increased stream flow and associated nutrient delivery (e.g., Justiæ et al., 2003), as well as reduced estuarine exchange time (Hagy et al., 2000; Smith et al., 2005). Elevated freshwater runoff associated with climatic events may, however, lead to more net heterotrophic conditions in shallow lagoons (Russell et al., 2006) and estuaries receiving high carbon loads from adjacent marshes or rivers (Jiang et al., 2008). Elevated temperature is expected to increase rates of evapotranspiration, which may balance or exceed increases in precipitation, causing reduced runoff. Conversely, changes in atmospheric pressure fields and associated wind patterns could decrease the intensity of upwelling-induced ecosystem production along many coastal shelf areas (e.g., Barth et al., 2007); changing winds could also contribute to changes in

stratification strength, as well as bottom O_2 pools and respiration rates. For example, historical analysis of P_n estimated for European coastal shelf communities revealed a positive relationship with climate-induced vertical mixing (Heath and Beare, 2008), while climate-induced changes in vertical mixing were associated with a decadal scale increase in subsurface R_n in the North Pacific (Emerson et al., 2004). Loss of coral reefs associated with ocean acidification could greatly diminish metabolic rates in these important ecosystems, but knowledge about coral reef resilience and climate-induced species shifts is lacking. Also, it is uncertain what alternative primary producer communities might replace corals. Because photosynthesis is generally less sensitive to temperature than respiration, global temperature increases will likely lead to lower P_n in the coastal ocean via elevated respiration (e.g., López-Urrutia et al., 2006; Harris et al., 2006). Other estuarine studies have linked elevated temperatures to reduced spring phytoplankton biomass, as temperature increases stimulated zooplankton grazing (Van Beusekom et al., 2009). In the open ocean, elevated temperature will likely decrease phytoplankton production, in part by enhancing stratification and reducing the mixing of nutrients into the photic layer (Behrenfeld et al., 2006).

Although it is clear that climate change will have significant impacts on organic matter production and consumption, the magnitudes, trajectories, and geographic distributions of these changes are poorly understood. The lack of understanding of these metabolic consequences of climate change is distressing, particularly because of the potential for positive and negative feedbacks that could reinforce or stabilize climatic changes. Future empirical and modeling studies should focus on improving knowledge about how rates and balance in ecosystem metabolism will respond to changing environmental conditions and alter the nature of estuaries and other aquatic environments.

15.8 CONCLUSIONS

Ecosystem metabolism represents an important measure of trophic status of estuarine and coastal regions, reflecting the combined catabolic and anabolic processes of all biological components of an ecosystem.

A wide variety of methods are available to measure different processes that contribute to ecosystem metabolism, ranging from continuous incubations to open-water changes in O_2 or TCO_2 to mass balance and model calculations. Each method has its own advantages and disadvantages.

Photosynthetic components of ecosystem metabolism are primarily driven by sunlight, water clarity, nutrient availability, temperature, the presence of toxic contaminants, and water exchange time.

Respiratory components of ecosystem metabolism are primarily driven by temperature and organic matter quantity and quality but are also influenced by water exchange time, especially when considering an entire system.

The magnitude and variability of ecosystem metabolism differs among coastal ecosystems, in response to water depth, species composition, and external organic matter sources, as well as to climatic controls and human perturbations.

Cross-system comparisons indicate a strong tendency for $P_n = 0$, but that coastal ecosystem metabolism varies widely between autotrophic and heterotrophic conditions. Shallow clear-water systems and larger open-water systems receiving high loads of inorganic nutrients relative to organic matter tend to be autotrophic. Enclosed, poorly flushed, and turbid ecosystems adjacent to wetlands or receiving high loads of anthropogenic organic material tend to be heterotrophic.

Future increases in coastal eutrophication will stimulate organic carbon production and likely push coastal ecosystems toward net autotrophy.

The effects of future climatic changes on ecosystem metabolism are uncertain. Alterations in precipitation, evapotranspiration, river flow, temperature, and atmospheric circulation could interact to cause large changes in coastal metabolism, either toward more autotrophic or heterotrophic conditions.

Future research should continue methodological development, while pushing for further investigations into how global environmental changes will affect metabolic balance in coastal ecosystems.

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CHAPTER SIXTEEN

ESTUARINE FOOD WEBS

James D. Hagy III and W. Michael Kemp

16.1 INTRODUCTION

Estuaries provide habitat for abundant plants, animals, and microorganisms, ranging from microscopic plankton (bacteria, yeasts, algae, protozoa) to larger benthic and pelagic organisms (seagrass, clams, crabs, sea trout, pelicans and dolphins). Estuarine biota can be characterized in a variety of ways including by taxonomy (e.g., algae, crustaceans, flounder), ecological function (e.g., primary producers, decomposers), and habitat and/or "niche" (e.g., benthic suspension feeders). These groupings are often the subject of distinct disciplines within estuarine ecology, whereas *food web ecology* examines their arrangements and interactions as a whole. Feeding habits are an integrative way to organize interactions among a diverse spectrum of organisms and functional groups, creating food webs. Like many areas of estuarine ecology, food web ecology developed first elsewhere and was later applied to estuaries. Important early studies in the field (Lindeman, 1942) focused on lakes. Early studies also examined planktonic food webs in the open ocean and interactions involving ocean fisheries (Ryther, 1969; Pomeroy, 1974). In this chapter, we examine some of the terminology, concepts, theory, and models that are used in the study of food webs in general and in food webs of estuaries in particular.

16.1.1 Food Chains and Food Webs

The transfer of food from the source through a series of organisms or groups of organisms eating each other has been referred to as a *food chain* (Elton, 1927). Figure 16.1 shows a simple food chain using energy systems language (Odum, 1967). At the base of the chain are the primary producers, depicted with a "bullet" symbol. In an estuary, the primary producers could be phytoplankton or other plants such as seagrasses, marsh vegetation, and benthic algae. Primary producers require inputs of matter and energy from external sources (depicted with a circle symbol). Arrows represent flows of either mass or energy, first to the herbivores and then to the carnivores, both of which are represented by hexagon symbols. Only a portion of the mass or energy produced in one compartment is transferred to the next, the remainder being transferred out of the food chain as export or emigration or dissipated as respiratory end products. In ecology, the term *trophic* (from the Greek word *trophikós*) refers to feeding or food. Thus, a group of organisms that are considered together because they are similar in their feeding habits and relationships may be called a *trophic group*. Transfers from one trophic group to another are called *trophic transfers*. *Trophic level* indicates the average number of trophic transfers required for food (measured as energy, nutrients, or organic matter) to reach the group starting from the primary producers, which are considered trophic level 1. In Figure 16.1, the trophic groups are at trophic levels 1, 2, and 3.

Rarely are trophic interactions (i.e., feeding interactions) as simple as depicted by a short food chain (Fig. 16.1). In most ecosystems, organisms feed on many different foods, often including both plants
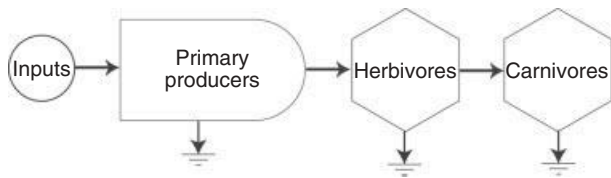
FIGURE 16.1 A simple food chain with three trophic levels illustrated using energy systems language (e.g., Odum, 1967; Odum, 1971). Arrows indicate transfer of matter or energy. Circles indicate inputs, which could include matter, such or nutrients, or energy. A ''bullet'' symbol indicates a primary producer, whereas hexagons indicate consumers. Horizontal lines (i.e., electrical ''ground'' symbols) indicate energy dissipation or recycling.

and animals, and this is particularly true for estuarine ecosystems. As our understanding of trophic relationships has increased, it has become necessary to think of trophic interactions as a *food web* rather than as a branching collection of food chains. One major reason is *omnivory*, which refers to the habit of consuming more than one type of food and potentially foods at different trophic levels. Species exhibiting omnivory are referred to as *omnivores* and are said to be *omnivorous*. A simple diagram of a food web (Fig. 16.2) illustrates omnivory and how it links food chains

together into a web. An increased appreciation of the importance of recycling nonliving organic matter (food energy), or *detritus*, is another reason for thinking of trophic relationships in estuaries in terms of a food web. Organic matter from either inside or outside an ecosystem may cycle several times between living organisms and detritus before being exported or dissipated through respiration. Early ecologists used the term *food cycle* to refer to these repeating or cycling flows of matter and energy. Detritus may be particularly important in estuaries because these ecosystems often receive significant inputs of organic matter from upstream terrestrial and freshwater ecosystems as well as from the coastal ocean.

16.1.2 Functional Groups and Trophic Guilds

Various terms are commonly used to describe the functional roles of organisms within food webs. *Primary producers*, also known as *autotrophs*, capture energy from an external source, usually the sun, to synthesize organic matter from carbon dioxide. Producers that use photosynthesis to generate organic matter are known as *photoautotrophs*. Because light is usually abundant in estuaries, photosynthesis tends to be by far the dominant organic matter source
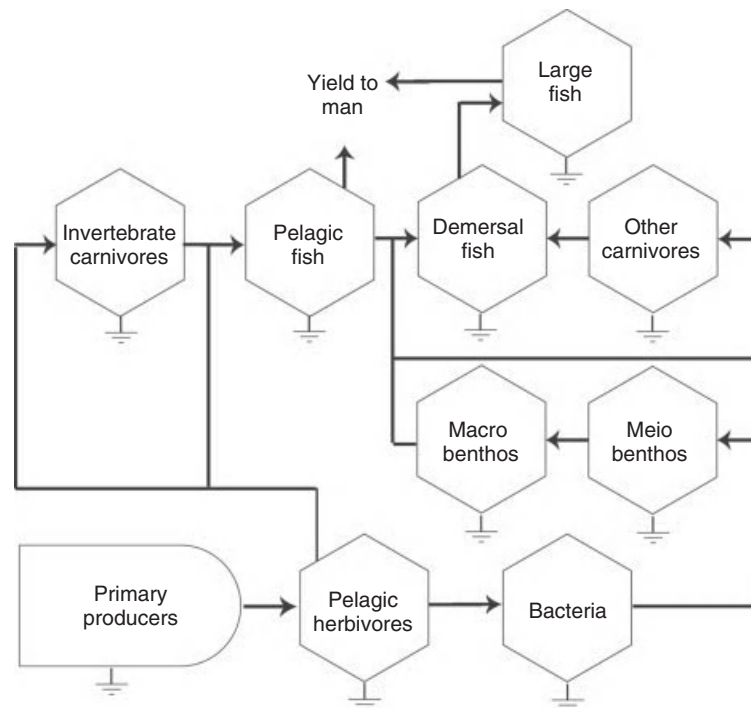
FIGURE 16.2 Energy flow in the North Sea food web (Steele, 1974) illustrating the complexity of a more realistic, but still simple, food web aggregated by ecological function rather than taxonomy. Some predators (e.g., demersal fish) consume prey from several prey groups. Similarly, some groups (e.g., pelagic herbivores, macrobenthos) are consumed by several different consumers. *Source*: Redrawn based on Ulanowicz and Kemp (1979).

to estuarine food webs. *Chemoautotrophs* use energy available from reduced inorganic chemical substrates, such as reduced sulfur compounds, to synthesize organic matter. Although there are entire food webs (e.g., in the deep sea) based on chemoautotrophy, it is much less important than photoautotrophy in estuaries. *Consumers*, also known as *heterotrophs*, obtain nutrition by consuming organic matter. Neglecting omnivory for the moment, consumers can be categorized according to their predominant trophic position relative to producers or detritus. Organisms functioning as *primary consumers* (1° consumers) are herbivores that consume primary producers directly. *Secondary consumers* (2° consumers) are carnivores that consume the primary consumers. Trophic positions can also be defined for higher-order consumers (e.g., 3°, 4°). *Mixotrophs* meet their nutritional and energy requirements through a combination of autotrophy and heterotrophy, for example, grazing to obtain nutrients and utilizing primary production to support energy requirements (Anderson et al., 2008).

These idealized trophic positions become somewhat blurred in real food webs, which include omnivores. For example, suppose that a group of organisms consume phytoplankton (a primary producer, trophic level = 1) as well as herbivores that graze on phytoplankton cells. This group would function as both a primary consumer (trophic level = 2) and a secondary consumer (trophic level = 3). Ecologists can determine a *fractional* or *average* trophic level by weighting, or apportioning, the feeding of the consumer to trophic levels 2 and 3. Supposing that it obtained 75% of its intake from phytoplankton directly and the rest from the other secondary consumer species, its average trophic level would be 2.25 $[= (0.75 \times 2) + (0.25 \times 3)]$, the mean trophic level at which the organism is feeding. The concept of fractional trophic levels has proved to be very useful for analyzing trophic relationships in estuarine food webs. As one example, the mean trophic level can be used to estimate how much primary production is needed to support a given production of consumers, or to consider the impact of human activites such as fishing on trophic structure (e.g., Pauly and Christensen, 1995; Pauly et al., 1998; Knight and Jiang, 2009).

Trophic guilds provide another useful way to describe the role of a group of organisms (Fig. 16.3) within a food web. These terms describe how the organisms feed, or on what type of food, with varying levels of specificity. For example, *scavengers* are *detritivores* that consume nonliving organic matter obtained from carcasses of dead animals. Important trophic guilds in estuaries include *planktivores* (plankton
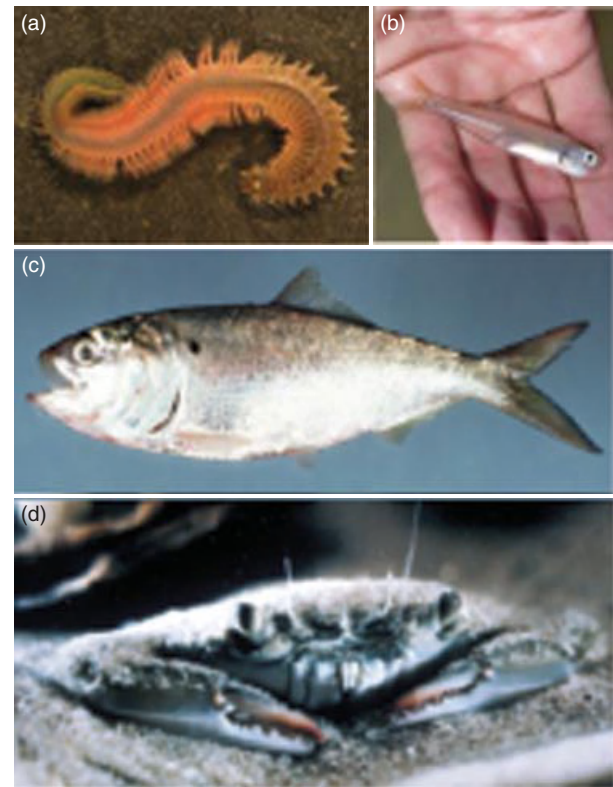
FIGURE 16.3 Estuarine species belonging to several trophic guilds. (a) The polychaete worm *Nereis succinea* is a generalist benthic deposit feeder that consumes small organisms near the sediment surface. (b) Bay anchovy (*Anchoa mitchilli*) is a small planktivore. (c) Atlantic menhaden (*Brevoortia tyrannus*) is a suspension feeding fish that consumes plankton. (d) The blue crab (*Callinectes sapidus*) is a benthic predator.

eaters), *benthivores* (consumers of bottom dwelling animals), and *piscivores* (fish eaters). *Suspension feeders* comprise a guild that obtains food by filtering out plankton and other small particles suspended in the water. Estuarine food webs may include both benthic suspension feeders, such as oysters or mussels, and pelagic suspension feeders, including specialized fish (e.g., Atlantic menhaden *Brevoortia tryannus*, striped mullet *Mugil cephalus*) or plankton such as the appendicularian *Oikopleura dioica* (Thomson, 1966; Alldredge, 1981). *Deposit feeders* ingest sediments, extracting the available nutrition and energy in the form of algae, bacteria, protozoa, or detritus. Feeding habits of some fish and invertebrates can change either with size and age (i.e., ontogenetically) or according to environmental conditions (Kanou et al., 2004). Others, such as the clam *Macoma balthica*, can switch feeding guild (e.g., from suspension feeding to deposit feeding) depending on the availability of different foods (Hummel, 1985).

FIGURE 16.4 A small purse seine vessel encircled a school of Gulf menhaden (*Brevoortia patronus*) near Pascagoula, Mississippi in June 1968. *Source*: Photo by R. K. Brigham, US National Oceanic and Atmospheric Administration.

16.1.3 Trophic Efficiencies

Efficiencies with which organisms assimilate food, grow, and transfer energy to organisms at higher trophic levels are important measures of food web structure and function. These are easily defined and understood as ratios of inputs to outputs for the bioenergetic budget. A simple equation can be written to describe this balance for an organism or a group of organisms.

$$C = P + R + U \qquad (16.1)$$

Consumption (*C*) is the amount of food ingested. A fraction of *C* is usually not fully used by the animal and is expelled (e.g., as feces) or excreted (e.g., as urine). Since excretion is often not estimated separately from egestion, the sum is represented as *unassimilation* (*U*). A portion of the assimilated matter and energy is used to produce new tissue (growth) or new organisms (i.e., reproduction) and is called *production* (*P*) of new biomass. *Respiration* (*R*) is the fraction devoted to supporting metabolic needs. Each of these quantities must be expressed in terms of a common measure, or currency, which for food webs in estuaries is usually energy, carbon, or nitrogen. Early studies of trophic transfers have focused on energy flow (e.g., Lindeman, 1942; Odum, 1957), whereas more recent studies have emphasized carbon (Baird and Ulanowicz, 1989), nitrogen (Baird et al., 2011), or even essential fatty acids or toxic contaminants. The following three measures of efficiency are related to these terms. (i) *Gross growth efficiency* (*GGE*) is the ratio of production (i.e., growth and reproduction) to consumption (*P/C*). *Assimilation efficiency* (AE) is the fraction of food consumed that crosses the gut of the consumer and contributes to its metabolism. This

may be thought of equivalently as

$$\frac{C - U}{C} \qquad (16.2)$$

or as

$$\frac{P + R}{C} \qquad (16.3)$$

The efficiency with which assimilated food is converted to production is net growth efficiency (NGE). NGE is equal to GGE/AE, but it is most commonly thought of as

$$\frac{P}{P + R} \qquad (16.4)$$

For example, *bacterial growth efficiency* (Section 10.3.2) is used in reference to bacteria and is defined in exactly this way (Valiela, 1995).

The terms defined above apply to the bioenergetics of single populations or trophic groups in isolation, whereas other related terms describe efficiency in the context of a food web. For example, *ecotrophic efficiency* (EE) refers to the fraction of production by a population or trophic group that is used within the food web at the next higher trophic level, harvested, or exported to another food web (Christensen and Walters, 2004). Low EE indicates that a large fraction of production is not used in the food web and is likely passed to detritus. *Trophic transfer efficiency* (TTE) is the fraction of production at one trophic level that results in production at the next higher trophic level. It may be helpful to think of TTE as the product of EE, AE, and NGE. Other common terms related to food webs include *consumption efficiency*, which is nearly identical to EE, and *production efficiency*, which is the same as NGE. Slobodkin (1960) estimated several efficiencies using the freshwater zooplankter *Daphnia pulex* feeding on the flagellated green alga *Chamydomonas reinhardtii* as a test case, concluding that "ecological efficiency is effectively constant" at approximately 10%. Although Slobodkin's ecological efficiency was defined in slightly different terms than the efficiencies defined in this chapter, and the estimate was based on relatively thin evidence, the 10% "rule of thumb" has been proved to be remarkably enduring: in a meta-analysis, Slobodkin's 10% estimate was close to the mean TTE for 140 aquatic food webs (Pauly and Christensen, 1995).

16.1.4 Food Chain Length

An interesting question about food webs is how many trophic levels are present and what limits the maximum number possible. Early ecologists suggested that there are usually at most five trophic levels

(Elton, 1927). However, recent studies have found trophic pathways with as many as eight steps (Baird and Ulanowicz, 1989; Hagy, 2002). Some ecologists have noted that very long food chains are possible when recycling of detritus is considered. A common convention to maintain detritus at a trophic level of 1 limits this possibility. Accordingly, the longest food chain within the food web shown in Figure 16.2 has a length of 8. However, no trophic group had an average trophic level greater than 5 because feeding via relatively short pathways was always important. One obvious reason for this limitation on food chain length is that substantial energy is dissipated (in respiration losses) with each trophic transfer. Even if the average TTE is a relatively high 20%, 1.6×10^4 units of primary production are required to support 1 unit of production at trophic level 6. Practically speaking, a species feeding exclusively at such a high trophic level is likely to be rare and quantitatively unimportant. From this standpoint, one might expect more trophic levels in food webs with high primary productivity. However, other factors could also affect the number of trophic levels. One hypothesis is that high trophic level pathways are likely to be unstable, limiting their prevalence (Pimm and Lawton, 1977), but this view remains a matter of debate (Sterner et al., 1997). Another consideration is the size of food. Particularly in the plankton, organisms usually capture and consume food only if it falls within a certain size range (Elton, 1927; Brooks and Dodson, 1965). The number of trophic levels could therefore depend on the size and feeding preferences of the important species. Because the species composition of phytoplankton in high productivity waters tends to be dominated by larger cells (e.g., diatoms), this may actually result in fewer trophic levels needed to produce carnivorous fish (Ryther, 1969; Landry, 1977). Many productive estuarine and coastal waters support stable fisheries harvesting large consumers at low trophic levels (Fig. 16.4). Examples include filter-feeding fish such as the Atlantic menhaden (*Brevoortia tyrannus*) and Pacific sardines (*Sardinops sagax*) and suspension-feeding bivalves such as Pacific oysters (*Crassostrea gigas*) and New Zealand green-lipped mussels (*Perna canaliculus*). These species principally feed as herbivores (trophic level = 2) or primary consumers (trophic level = 3) and therefore, have an average trophic level between 2 and 3 (Pauly et al., 1998). These filter-feeding animals have a "telescoping effect" (Elton, 1927), wherein relatively large organisms feed on very small ones, leading to increased trophic transfer efficiencies and potentially shorter food chains (e.g., blue whales and whale sharks).

16.2 PORTRAYING FOOD WEBS

16.2.1 Ecological Pyramids

Different approaches have been used to examine the structure of food webs. One approach is to examine graphically the relative magnitude of abundance, biomass, or productivity across trophic levels using *ecological pyramids* (Odum, 1971). The shape of a pyramid reflects differences in the food web and characteristics of the dominant taxa. The "pyramid of numbers" is particularly affected by the dominant taxa and provides less insight into community structure than other types of pyramids. On the other hand, the pyramid of biomass is more interesting, potentially revealing substantial differences in structure. For example, a biomass pyramid for a lake in Wisconsin has a significant biomass of primary producers and much lower biomass of consumers (Fig. 16.5). In contrast, the biomass of primary consumers exceeds the biomass of producers in the English Channel. This "inverted pyramid" suggests that the producer biomass is rapidly replaced by growth (i.e., higher productivity, lower biomass), while biomass accumulates slowly in longer-lived consumer organisms. Production or energy flow pyramids must be wider at the bottom trophic level because a fraction of energy and biomass is lost from the food web with each transfer to a high trophic level. Ecological pyramids may also illustrate the fraction of energy flow in the primary consumers that depends on detritus, rather than direct grazing on primary producers, as in the example from Silver Springs (Fig. 16.5).

16.2.2 Projecting Food Webs to Food Chains

One problem with ecological pyramids is that they are predicated on the existence of discrete trophic levels (i.e., 1, 2, 3), when many organisms in fact feed at more than one trophic level and therefore feed at noninteger or fractional trophic levels. Consequently, ecological pyramids have not been used extensively in recent work on estuarine food webs. One way to approach the problem of representing feeding at fractional trophic levels is to apportion feeding to one of several "virtual integer trophic levels," which are also sometimes called *canonical trophic levels*. For example, species that feed 50% at trophic level 2 and 50% at trophic level 3 would have a fractional trophic level of 2.5. Mathematical procedures for this analysis (Ulanowicz and Kemp, 1979) are now part of the methods known collectively as ecological network analysis (Section 16.6). Figure 16.6 illustrates the effective food chain obtained by projecting the

Pyramid of biomass (grams dry weight per square meter)

Pyramid of energy flow (kcal/m^2/year)
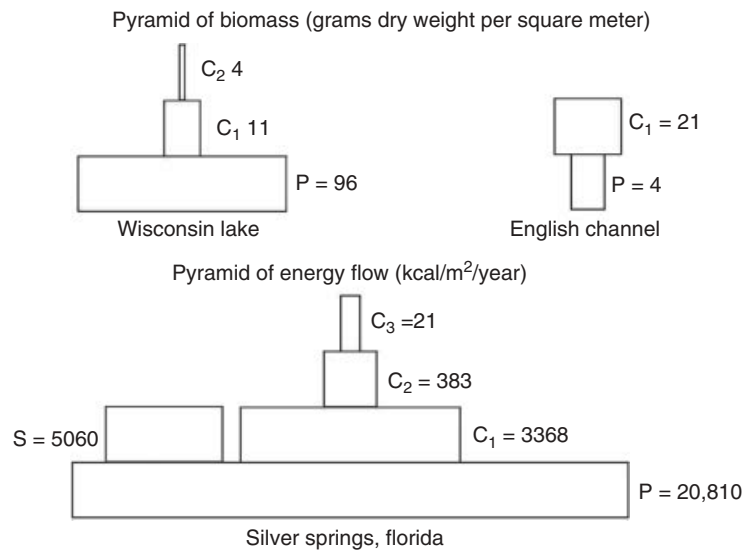
FIGURE 16.5 Ecological trophic pyramids of biomass and energy flow (i.e., production at each trophic level). P = primary producers, C_1 = first consumers (herbivores), C_2 = second consumers (first carnivores), S = saprotrophs (detritivores, feeding on detritus or dead organic matter). Note the convention of placing primary producers as the bottom block of the pyramid and top carnivores as the highest block. *Source*: Redrawn from Odum (1971).
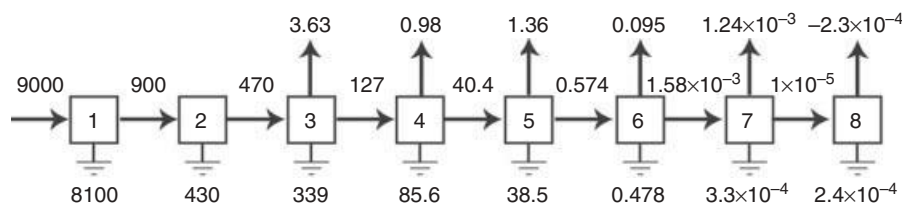
FIGURE 16.6 The effective food chain for the North Sea food web network (Steele, 1974) depicted in Figure 16.2. Flows, which in this case are energy flows in kilocalories per square meter per year, are apportioned to integer trophic levels following the method of Ulanowicz and Kemp (1979). Flows from an integer trophic level to the next indicate upward transfer of energy within the food web. Flows to ''ground'' are defined as in Figure 16.1, where respiration is combined with flows to detritus and loss from the food web. Additional flows can be included in the effective food chain to explicitly represent the return of detritus to the food web. Upward arrows represent the yield to humans at each effective trophic level. Not surprisingly, the largest yield to humans occurs via the shortest and most efficient trophic pathway (boxes 1–3), which in this example is primary producers → pelagic herbivores → pelagic fish (Fig. 16.2).

North Sea food web (Steele, 1974) from Figure 16.2 onto a series of canonical trophic levels. This analysis illustrates several key features of the food web, such as the length of the longest trophic pathway (i.e., eight trophic steps) and that most flow is confined to the first five trophic levels. In addition, Figure 16.6 shows that 10% of primary production is transferred to the second trophic level, whereas more than 50% of the input to trophic level 2 is transferred to trophic level 3. We also see that much of the yield to humans occurs at the lowest exploited trophic level (i.e., the lowest trophic level subject to fishing), even though fishing extracts a relatively small fraction of total production at the lower trophic levels. Projecting food webs into food chains provides a useful approach for characterizing the overall food web structure.

16.2.3 Trophic Spectra

Darnell (1961) introduced the *trophic spectrum* as a tool to illustrate graphically his detailed data on the food habits of organisms in Lake Pontchartrain, an estuarine lake in the Mississippi delta (Fig. 16.7). Among his key observations was that food habits of species often change as they develop through different life stages and as they increase in size (i.e., diet changes *ontogenetically*). Darnell's trophic spectrum also showed the great diversity of food (i.e., the prevalence of omnivory) in most diets, with few species being
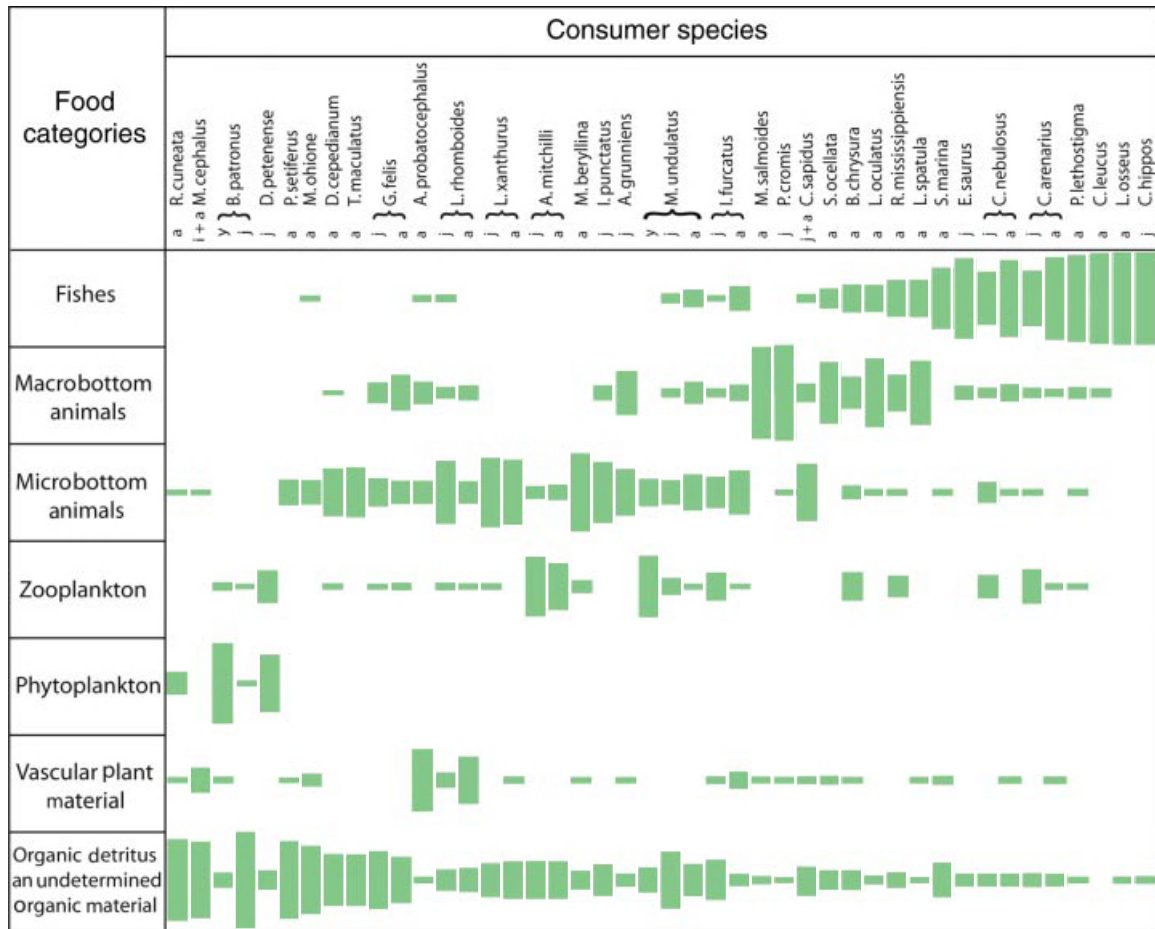
FIGURE 16.7 Trophic spectra for the most important consumer species of Lake Pontchartrain, indicating the feeding habits of each of the consumer species listed across the top. As an example, the bivalve *Rangia cuneata*, in the first column, largely consumes organic detritus, plus some phytoplankton. In contrast, *Caranx hippos*, a marine fish in the jack family, consumes fish almost exclusively. *Micropogonias undulatus*, or Atlantic croaker, has more varied food habits than either of these species, consuming a mixture of fish, small benthic ("bottom") animals, zooplankton, and organic detritus. *Source*: Redrawn from Darnell (1961).

highly specialized in their food habits. Many species included significant quantities of organic detritus in their diets. Omnivory and detritivory are usually important in estuarine food webs. This appears to result from several factors: (i) the unpredictable availability of specific food items, (ii) the fact that estuaries often receive significant inputs of detritus from terrestrial sources, and (iii) the tendency for physical processes in estuaries to retain and concentrate particulate detritus. An additional methodological factor is that unidentifiable food items may be considered to be "detritus."

16.2.4 Biomass Body-Size Spectra

Biomass body-size spectra show the distribution of biomass as a function of logarithmic body size classes

for all organisms in an ecosystem or habitat. Ecological analysis based on size spectra has developed from early observational work into a well-developed body of theory and predictive science (Kerr and Dickie, 2001). Interpretation of biomass spectra is based on the assumption that they reflect transmission of matter and energy through trophic interactions in which large organisms generally consume smaller organisms as prey (Elton, 1927). Early biomass spectra focused on microscopic plankton in the world's oceans (Sheldon et al., 1972), which showed surprising uniformity in biomass across size classes (i.e., flat spectra), prompting further empirical and theoretical investigations. Systematic differences in spectra across a gradient of latitude in the South Atlantic Ocean suggested that size-spectra might reveal important characteristics of ecosystems as well

as differences among and within them (Sheldon et al., 1972). Platt and Denman (1977) introduced the normalized biomass spectrum, in which the biomass in a size-class is divided by the width of the size class. The slope of normalized spectra tends to have a characteristic value of approximately −1.0 compared with the relatively low slope (i.e., flat) for size spectra that are not normalized. An advantage of normalized spectra is that their shape is independent of the width of the intervals, making these spectra well suited to comparing different ecological systems.

Research using biomass spectra has shown that spectra often have one or more size ranges in which there is very little biomass, creating the appearance of distinct ''domes'' or biomass modes within the spectrum (i.e., specific size classes that occur more frequently). The investigators who first identified these structures within biomass spectra for plankton communities suggested that they represent physical limits on the possible sizes of plankton species. Subsequent investigators noted that domes of high biomass in benthic spectra complemented size ranges with low biomass in the plankton, suggesting coupling of planktonic and benthic food webs (Kerr and Dickie, 2001). Jung and Houde (2005) made a related observation using size spectra for fish communities in the Chesapeake Bay (Fig. 16.8), finding that the ''dome'' of biomass representing piscivorous fish could not be explained solely on the basis of the biomass of smaller zooplanktivorous fishes. Rather, they suggested that the diet of the larger species was supplemented by consumption of benthic invertebrates (Jung and Houde, 2005).

16.3 TROPHIC THEORY

The populations and communities that compose estuarine food webs interact in numerous ways, including both direct and indirect feeding relationships. In this section, we focus on trophic interactions as they appear in estuarine food webs. Although interactions are described for convenience as occurring between ''species,'' the terminology applies equally to groups of species such as trophic guilds.

16.3.1 Direct Trophic Interactions

There are five types of direct trophic interactions: *competition, predation* or *parasitism, mutualism, commensalism*, and *amensalism*. These interactions are defined on the basis of the effect of the interaction on each of the species involved. *Competition* is an important interaction that has a negative effect on each species.
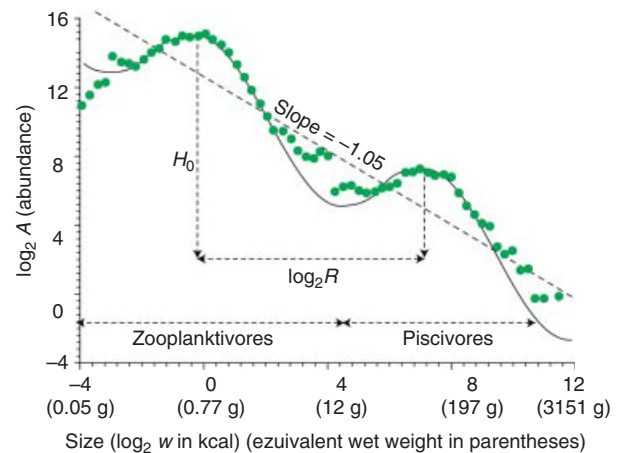
FIGURE 16.8 A normalized biomass size spectrum for fish captured in the Chesapeake Bay. The graph depicts the abundance of fish within size ranges normalized by the width of the size range. The normalized spectrum is characterized as having two distinct trophic groups, which appear as ''domes.'' The first dome corresponds to bay anchovy (*Anchoa mitchilli*), the dominant zooplanktivore, and the second dome corresponds to the larger piscivores such as striped bass (*Morone saxatilis*). Bay anchovy account for a significant fraction of the diet of the piscivores. *Source*: Redrawn from Jung and Houde (2005).

In the context of food webs, direct competitors are usually two or more species that derive a substantial fraction of their diet from the same food resource. Intraspecific competition is also an important factor structuring population dynamics (e.g., density dependence in fish populations).

Predation and *parasitism* each describe interactions in which one species benefits from the interaction, to the detriment of the other. In the case of predation, the predator completely consumes the prey. Predation is ubiquitous in nature and is a key factor structuring most estuarine food webs. Parasites negatively affect the species they live in, on, or in association with (i.e., their *host*), but they generally do not immediately kill the host. Instead, parasites obtain food by consuming a portion of the host or a portion of the diet obtained by the host. While parasitism is very common and potentially very important (Thompson et al., 2005), the effect of parasite–host interactions on food webs and the best way to represent parasites in food web models are not well understood (Lafferty et al., 2008). For example, a parasite might simply impair its host and contribute little to the food web, or it could as a prey species support additional trophic pathways within the food web.

Mutualism is a direct interaction in which both species benefit from the interaction. *Commensalism*

is related, but one species benefits from the interaction and the other is unaffected. *Amensalism* is an interaction that is detrimental to one species and has no effect on the other. These interactions are not as ubiquitous within estuarine food webs as competition and predation but may still be very important. Often they appear as nontrophic relationships. For example, the eastern oyster *Crassostrea virginica*, creates an entire habitat structure, providing ample opportunity for *commensals*, species that use the structure and excess particulate organic matter concentrated by the oysters, but have little direct effect on the oysters. Similarly, fiddler crabs and marsh cordgrass (i.e., *Spartina*) each benefit by the other's presence, an example of mutualism related to habitat structure rather than trophic interactions (Bertness, 1985).

16.3.2 Indirect Trophic Interactions

Indirect trophic interactions involve interactions between two species that are mediated by interactions involving other species. Analysis of estuarine food webs often reveals many indirect trophic interactions. In an example of ''top-down control'' in a food web, feeding activity of predators on planktonic herbivores can result in positive effects on phytoplankton by reducing grazing pressure. Indirect trophic interactions can sometimes overwhelm direct interactions. For example, a predator can have a net positive impact on productivity of its own prey, making it a ''beneficial predator'' (Ulanowicz and Puccia, 1990). Consider the sea nettle *Chrysaora quinquecirrha* (Fig. 16.9), a predator that not only consumes zooplankton, fish eggs, and larvae (Purcell, 1992) but also preys very efficiently on the ctenophore *Mnemiopsis leidyi* (Purcell and Cowan, 1995). Since *Mnemiopsis* can become very abundant and is a voracious predator on zooplankton (Purcell et al., 2001), the net effect of *Chrysaora* on zooplankton can be positive because of its effective control of *Mnemiopsis* (Breitburg and Fulford, 2006; Testa et al., 2008). Selective predation on diseased prey can also benefit a prey population by preventing disease epidemics. This dynamic is well recognized among terrestrial wildlife and has also been identified in lake food webs (Duffy et al., 2005). Other examples of beneficial predation have been identified, illustrating the importance of predators for maintaining healthy ecosystems (Bondavalli and Ulanowicz, 1999).

The concept of *keystone species* also relates principally to indirect trophic interactions. As originally suggested by Paine (1966, 1969), the keystone species is a high trophic level predator whose presence or abundance has a large effect on the structure and persistence of the community. A keystone predator is not necessarily abundant, but it may be. Libralato et al. (2006) defined keystone species as ''a relatively low biomass species with a structuring role in their food web''. A keystone species generally alters the outcome of competitive interactions among species at lower trophic levels, possibly preventing exclusion of one or more competitors by the otherwise dominant competitor. Although ecologists have further developed this concept (Mills et al., 1993), applications in the context of estuarine food webs have been limited. Libralato et al. (2006) developed a quantitative measure of ''keystone-ness'', derived from analyses of trophic networks, which they argue could improve application of the concept to conservation biology. Tsagarakis et al. (2010) applied this approach to coastal systems in the northern Mediterranean and concluded that mesozooplankton were quantitatively most like a keystone species.

FIGURE 16.9 The cnidarian *Chrysaora quinquecirrha* occurs in many estuaries. *Source*: Photo by Anastasia Shesterinina.

16.3.3 Trophic Cascades

The idea of cascading trophic controls traces back at least as far as Hairston et al. (1960), who explained, among other observations, how trophic controls may be responsible for terrestrial plant communities being generally intact and green rather than defoliated by grazers. Carpenter et al. (1985) used the term ''trophic cascade'' referring to how trophic interactions impact algal biomass in lakes. An example three-trophic-level pelagic food chain might include phytoplankton as primary producers, zooplankton as herbivores grazing on phytoplankton, and small carnivorous fish consuming the zooplankton (Fig. 16.1). In this example, fish biomass and production is limited only by the production of its prey and is said to have *bottom-up control*. In contrast, the zooplankton grazer is also subject to *top-down control*, since predation by fish can limit its biomass. Control of grazers via predation is likely to cause phytoplankton abundance to be controlled by resource limitation (i.e., availability of nutrients). This theory has been generalized as the ''exploitation ecosystem hypothesis,'' which predicts that even numbers of trophic levels (e.g., 2 or 4) will lead to lower standing biomass of plants compared to odd numbers of trophic levels (1 or 3; Polis and Strong, 1996). Trophic cascade theory also suggests that increased predation by organisms at the top of a 5-trophic-level food chain will cause decreases and increases in alternating levels down to primary producers (levels 4 and 2 decrease and levels 3 and 1 increase); these responses will also be increasingly attenuated down the food chain (Carpenter et al., 1985).

Although the concepts of trophic cascades and top-down versus bottom-up control have their place in the literature describing trophic dynamics of estuaries, the two key questions are how important these are in the dynamics of food webs, rather than food chains, and to what extent food webs in estuaries should be expected to exhibit trophic cascades. Several attributes of estuarine food webs may in fact tend to reduce the importance of trophic cascades in estuaries (Borer et al., 2004). Omnivory, which we have suggested often characterizes the food habits of estuarine animals, may reduce cascades, which are strongest in food chains involving trophic specialists (i.e., narrow and static diet composition) and weaker when species have omnivorous and dynamic (i.e., opportunistic) food habits (Polis and Strong, 1996). Strong coupling of benthic and pelagic food webs may also limit trophic cascades, since environmental factors and trophic dynamics may impact these areas of the food web differently. Another important factor

limiting trophic cascades in estuaries is their openness. Predators and prey in estuaries can migrate between estuaries and open coastal waters (Sackett et al., 2007) and are subject to external controls during their period of nonresidence. Strong physical controls such as changes in the inflow of freshwater and nutrients into estuaries can also impose short-term variability on lower trophic levels, overwhelming internal biological controls, and preventing clear expression of top-down effects on phytoplankton via trophic cascades.

These considerations notwithstanding, there are at least a few examples of trophic cascades in coastal marine systems. A well-cited example is the decimation of kelp forests because of sea urchin grazing, which followed a decline in sea otters (Estes et al., 1999). In another example, an increase in phytoplankton abundance in Patuxent River estuary occurred despite decreased nutrient inputs (Testa et al., 2008). The authors' analysis suggested that a trophic cascade was involved, wherein decreased abundance of a top gelatinous predator led to increased abundance of a zooplanktivorous intermediate predator, reduced abundance of herbivorous zooplankton, and finally, increased phytoplankton abundance. In general, estuarine food webs are affected by both bottom-up and top-down controls (Heck and Valentine, 2007), but examples of strong cascades are relatively rare (Micheli, 1999).

16.4 ATTRIBUTES OF ESTUARINE FOOD WEBS

16.4.1 Spatial Mosaic of Coastal Habitats

In many instances, the structure of estuarine food webs is regulated by the complex spatial mosaic of different habitat types that characterize the ecosystem (Heck et al., 2008). The ''coastal ecosystem mosaic'' (Sheaves, 2009) includes distinct habitat types such as open-water pelagic, tidal creeks and channels, seagrass meadows, oyster or mussel beds, coral reefs, intertidal sand or mud flats, rocky shores and deeper platforms, and emergent tidal wetlands including salt marshes and mangroves. The estuarine salinity gradient also creates distinct habitats defined by salinity. Although each of these habitats supports distinct biological communities, they are also connected within the overall food web by fluxes of matter and energy across the spatial mosaic. Mechanisms of spatial coupling frequently include physical exchange of water and associated plankton and detritus and

movements or migration for the purpose of feeding, spawning, and other ontogenetic changes. The latter has been referred to as the ''trophic relay'' hypothesis, which has been used to describe mechanisms coupling intertidal salt marshes and adjacent subtidal habitats (Kneib, 1997).

One of the most widely relevant examples of spatial linkage within estuarine food webs is coupling of benthic and planktonic (or pelagic) food webs. Extreme depth of water prevents such coupling in the deep sea, whereas the relatively shallow nature of most estuaries favors benthic–pelagic coupling. The estuarine benthos usually consume a significant fraction of total organic inputs to estuaries (∼25%; Nixon, 1982). Benthic filter feeders, which benefit from the constant motion of water associated with tides, can exert grazing control over phytoplankton production and biomass (Cloern, 1982; Nixon, 1988). Suspension- and deposit-feeding benthos contribute significantly to the diets of benthopelagic predatory fishes such as red drum (*Scaenops ocellatus*) and Atlantic cod (*Gadus morhua*). Some of these benthivorous (i.e., benthos-eating) species are prey for top pelagic predators, some of which also consume macrobenthos directly (Hartman and Brandt, 1995; Tsagarakis et al., 2010). Finally, direct herbivory (by fishes, turtles (Jackson, 2001), marine mammals, e.g., manatees, and birds (Heck and Valentine, 2006) on benthic primary producers, including microalgae, macroalgae, and seagrasses, links shallow benthic communities to overall estuarine food webs (Choy et al., 2008).

Heck et al. (2008) illustrate how highly productive shallow-water seagrass habitats are often relatively important to the food webs of surrounding habitats within estuaries (Fig. 16.10). For example, some fish live in mangroves but feed in seagrass meadows, resulting in trophic flows from seagrass to mangrove habitats. Similarly, some reef resident fishes feed in seagrass meadows, generating net fluxes of organic matter and nutrients to reef areas and their associated food webs. In temperate estuaries, various fishes feed in both salt marshes and seagrass beds, while juvenile blue crabs use seagrasses for feeding and shelter before migrating elsewhere as adults (Heck et al., 2008). Tidal marshes also provide physical habitat and food for omnivorous consumers. For example, in coastal Louisiana, the regional distribution of shrimp abundance and production is proportional to the length of marsh/open water interface (Haas et al., 2004). In some cases, the value of different habitats for a particular group in a food web can be defined in terms of competing needs of refuge from predation and access to food. This is an important way by which the spatial habitat mosaic structures trophic interactions in estuarine food webs (Walters, 2000).

16.4.2 The Importance of Detritus

Early work investigating productivity of marine food webs was strongly influenced by work describing a grazing food chain in which phytoplankton production is directly grazed by herbivorous zooplankton, linking microplankton production to pelagic food webs. Research along the southeast coast of North America, however, showed that this model was inadequate to describe trophic flows in some estuaries. Large tides in these coastal systems, which are fringed by extensive salt marshes, promoted vigorous material exchanges between marshes and open water habitats. Significant quantities of production by marsh grasses was not grazed as living material, but instead was passed to a ''detritus food chain'' where the decaying material was consumed and directed into productive trophic pathways (Odum, 1971; Choy et al., 2008; Galván et al., 2008). Similarly, Darnell (1961), whose work we have already mentioned (Fig. 16.7), observed that detritus accounted for a fraction of the diet in nearly all the species analyzed, with the exception of the top piscivorous (i.e., fish-eating) predators. By the early 1960s, detritus was recognized as an important energy source in nearly every type of aquatic ecosystem. Detritus may be especially important in estuaries because they receive significant external inputs of detritus (i.e., allochthonous carbon) from adjacent terrestrial and oceanic ecosystems. Estuarine ecosystems may also generate significant quantities of vascular plant detritus from seagrass meadows, marshes, and mangroves within the littoral and intertidal zones (Teal, 1962; Odum and de la Cruz, 1963). Food webs in shallow tropical estuaries fringed by mangroves tend to be supported by decomposing plant material and associated microbes, with the types and sizes of materials used varying by consumer (Odum and Heald, 1975; Fig. 16.7). Ultimately, lability and nutritional value are as important as the quantity available for determining the importance of the contribution of detritus to activity in an estuarine food web (Cebrian, 1999).

Although simple in concept, quantifying trophic flows involving detritus can become surprisingly complicated. For example, particulate detritus is often colonized by algae, bacteria, and meiofauna, forming a complex of biota and detritus whose nutritional and elemental composition (e.g., C/N ratio) differs from that of the detritus alone. The complex and numerous functions of microbes in estuarine ecosystems are addressed in Chapters 9 and 10. Here we

note that microbes mediate a very slow biogeochemical "aging" of detritus, breaking down the most recalcitrant compounds (e.g., lignin) and eventually improving their nutritional value to consumers (Tenore et al., 1984). Given adequate time for processing, detritus can be processed repeatedly until the material is ultimately buried or otherwise exported, thereby increasing the potential importance of detritus in estuarine food webs.

16.5 CONSTRUCTING FOOD WEB MODELS

Estuarine food webs are complex, dynamic, and open. To understand these complex systems better, it is often useful to construct models of the system that can be analyzed quantitatively. A good first step in modeling estuarine food webs is to select the temporal and spatial scales of interest. This section emphasizes models that address at least a seasonal time scale and some sort of spatial average. This leaves for the future a discussion of explicit modeling of patchy and variable food web dynamics. The second step is defining research questions to be addressed with the food web model. Next, the modeler must choose the currency for the food web (e.g., energy, carbon, nitrogen), the *nodes* (feeding groups) to include, and the important trophic interactions or *flows*. Finally, the investigator must compile relevant data and ecological information to quantify the food web. These steps may all be taken iteratively and interactively. For example, ecological information being collected to describe the food web as initially planned may reveal that an additional node is needed or that a node may reasonably be omitted.

There are two basic approaches to calculating trophic flows for a food web model. The first, which is called the *a priori* approach, involves estimating all the flows from empirical data. The second approach is called *inverse modeling* and involves writing a series of equations or inequalities that constrain the possible solutions (i.e., the estimates for the flows) and then solving for the missing quantities using matrix methods. In some applications, the known quantities were primarily biomasses plus estimates of a few flows (e.g., primary production and sedimentation) and a set of physiological constraints (Vézina and Platt, 1988). Recent applications have addressed more complex systems with more constraints, taking advantage of improved computational resources (Leguerrier et al., 2004). Inverse methods have also been used to solve for biomasses, rather than flows (Polovina, 1984), and to estimate solutions when several different types of information were unknown (Christensen and Pauly, 1992). In some cases, statistical methods can be used to find a best fit solution given the data and constraints (Christensen and Pauly, 1992). Other analyses have employed elements of both approaches, for example, by developing initial *a priori* estimates of flows and then adjusting flows using a "balancing" algorithm to achieve mass balance (Allesina and Bondavalli, 2003; Christensen and Walters, 2004). The following several sections present details of constructing estuarine food webs.

16.5.1 Choosing the Appropriate Scale and Currency

Key decisions in food web model development involve defining the temporal and spatial extents of the model and the resolution of its trophic groups. The appropriate choices depend on the research questions of interest. The spatial extent is the area (or water volume) under consideration for the analysis and may be an entire estuary (e.g., Rybarczyk et al., 2003) or a region of an estuary (e.g., Carrer and Opitz, 1999). Temporal extent defines a period from which data are being considered, usually ranging from a single season to an entire decade (Baird and Ulanowicz, 1989). The spatial and temporal scales should be large enough to encompass the ecological features of interest and the associated food webs. In general, the "currency" of the food web can use flows of energy (Dame and Patten, 1981) or flows of mass, such as carbon (Baird and Ulanowicz, 1989), nitrogen (Christian et al., 1996), or wet weight biomass (Manickchand-Heileman et al., 1998). Regardless of the choice, models developed in one currency may reflect implicitly the importance of other flows in other currencies. For example, if growth is limited by low nitrogen content of food, rather than carbon, this may be reflected in a carbon-based food web analysis as low carbon growth efficiency. The discussion below is most applicable for food webs using carbon or energy as currency. Generally, the availability of information for constructing food webs in terms of nitrogen or phosphorus is more limited than for carbon or energy.

16.5.2 Composition of the Food Web (Nodes)

Another important step in developing a food web model is deciding what to include in the food web and how to represent it. An almost universal attribute
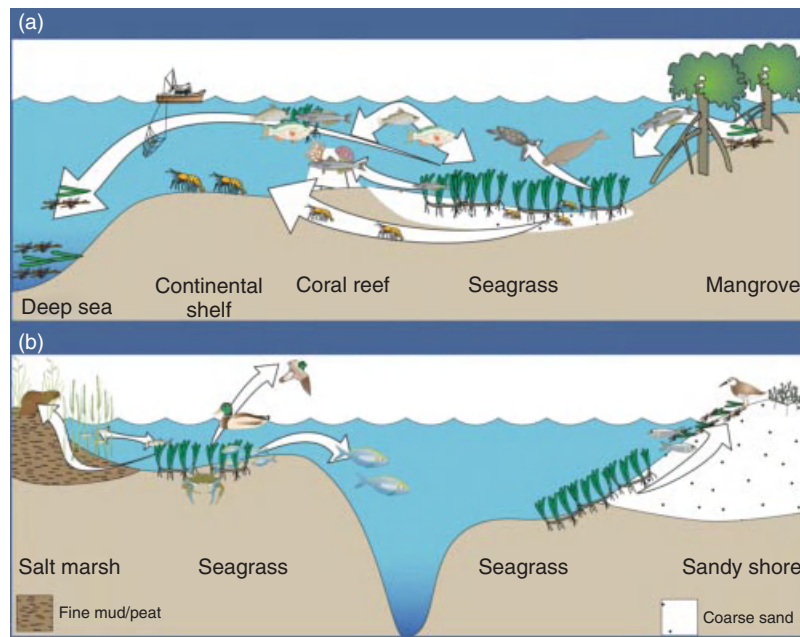
FIGURE 16.10 Mechanisms of trophic transfers from seagrass meadows to adjacent coastal habitats in (a) tropical and (b) temperate regions. *Source*: Modified from Heck et al. (2008).

of food web models is their uneven level of aggregation of species across communities and trophic levels. Lower trophic levels are usually represented as broad groups of similar species (e.g., zooplankton) or feeding guilds (e.g., suspension-feeding benthos), whereas upper trophic levels are often resolved to the species level. This tendency is primarily driven by availability of data, but may also reflect the questions of interest. To represent a trophic node (group of organisms with similar diets) in the food web model, it is necessary to quantify the magnitude of production, magnitude and composition of diet, and fate of the biomass that is produced (e.g., who consumes it). This information is usually not available for individual planktonic or benthic species but may be estimated for groups of species or feeding guilds. Species-level definition of organisms at higher trophic levels can provide key insights into food web dynamics. For example, by combining two distinct groups of sharks (pelagic and benthic feeding) into a single aggregated node, the resulting ''super shark'' group had an unrealistically broad impact on the food web, even though neither type of shark has as large a trophic effect (Friere et al., 2007). Food web models are sometimes focused on particular groups of consumers, ranging, for example, from microplankton (Baird and Ulanowicz, 1989), to gelatinous zooplankton (Tsagarakis et al., 2010), to fisheries (Manickchand-Heileman et al., 1998). In other cases,

food web models reflect broad interest in ecosystem-level structure (Rybarczyk et al., 2003). Although a variety of food web structures and approaches may be legitimate, the level of aggregation chosen for the food web model can also have substantial impact on the results (e.g., Martinez and Lawton, 1995).

16.5.3 Organism Abundance and Biomass

Even though trophic networks are defined by flows between nodes, estimation of the abundance or biomass (or both) of organisms is a key step in constructing food webs. The reason is that, for most trophic groups, flows are often computed as a function of biomass. Exceptions include phytoplankton and bacteria production rates, for which direct measurements are often available for community production rates (Parsons et al., 1984; Kemp et al., 1993). The biomass of zooplankton and benthos may be based on plankton net tows or sediment grab samples. Trawl sampling is commonly used to quantify the ''relative abundance'' and biomass of fish, but direct measurement of fish abundance is difficult. Sometimes it is possible to infer fish abundances indirectly, such as from production of fish eggs (Rilling and Houde, 1999). For exploited fish populations, virtual population analysis (Gulland, 1965) can be used to infer population size, given the size and age structure of the catch and other parameters (e.g., natural mortality rate).

16.5.4 Bioenergetic Rates

The flows of food between the nodes (feeding groups) effectively define the food web. As discussed in Section 16.1.3, critical rates are related to each other by the bioenergetic equation for an organism, population, or feeding group, where consumption (C) is equal to the sum of production (P), respiration (R), and excretion plus egestion (U). All these rates are needed for each node. A good approach (called *allometry*) is to use physiological equations and ratios, which vary consistently with organism size. For example, annual production (P) of individual populations or whole communities can be computed from average population biomass (B) and an estimate of average individual organism biomass (M). The allometric equation:

$$\frac{P}{B} = 0.65 M_s^{-0.37} \tag{16.5}$$

applies across a 10^5-fold range in body size (M_s, units are body mass converted to energy equivalents in kilocalories) for a diversity of taxa (e.g., Banse and Mosher, 1980; Fig. 16.11). Similar relationships between organism physiology and size have been reported for all bioenergetic rates (e.g., Harris et al., 2006). Thus, respiration can be estimated using allometric equations or empirical relationships between respiration and consumption. The NGE:

$$NGE = \frac{P}{P + R} \tag{16.6}$$

can also be used to compute R, given an estimate of P. Detailed review of the literature on NGE for aquatic organisms suggests a typical value of approximately 60% (Schroeder, 1981).

The final term needed to describe a bioenergetic balance is the combined egestion and excretion rate, sometimes referred to as *unassimilation*, or U. Similar to NGE, generalizations about U are possible for different classes of organisms (Schroeder, 1981), depending on diet and particularly food quality. A diet may include large fractions of indigestible molecules (e.g., cellulose) or animal parts (e.g., bones or feathers), leading to lower AE. Differences in elemental composition of a consumer and its food may limit assimilation, where, for example, a herbivore with a carbon to nitrogen ratio lower than its diet (e.g., herbivorous fish) will tend to have lower carbon AE (Elser and Urabe, 1999). Note that depending on the application, this combined treatment (as U) of egested food, which has not been fully processed, and excretion of metabolic wastes may be unsatisfactory.
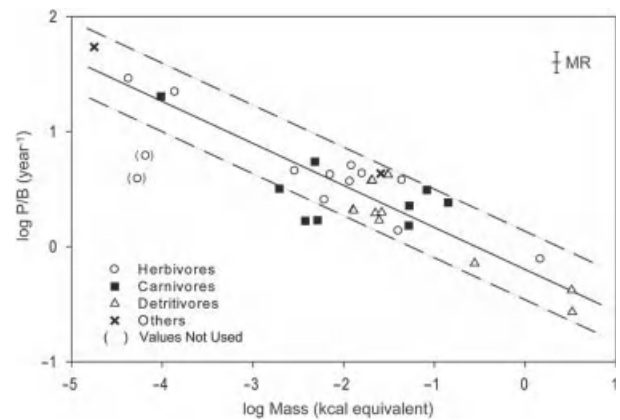
FIGURE 16.11 Relationship between log(body size at maturity) and log(P/B) (annual production/biomass) for a variety of functional groups of species. The equation for the solid regression line is log(P/B) = $-0.19 - 0.27$ log(M). Dashed lines indicate 50% and 200% of the predicted P/B. Body size is converted to energy content (i.e., caloric) equivalents. The relationship spans 5 orders of magnitude in body size. MR refers to the mean range in P/B for 16 species with multiple observations. *Source*: Redrawn from Banse and Mosher (1980).

16.5.5 Food Habits

To construct a food web model, it is essential to have quantitative data on the diets of each feeding group that can be used to partition total consumption for each node into contributions obtained from each of the other nodes. Three broad categories of empirical methods for obtaining diet information include (i) analysis of stomach contents, (ii) feeding experiments, and (iii) chemical biomarkers. Stable isotopes are a particularly useful form of chemical marker for analysis of estuarine food webs, and these are examined separately in the next section.

Quantitative analysis of the contents of stomachs of individual organisms, referred to as *gut contents analysis*, involves visual identification and measurement of all food materials in the stomachs of sample organisms. This is one of the earliest and most widely applied approaches for examining food habits. For example, the study by Darnell (1961) on food habits of consumers in Lake Pontchartrain, Louisiana, largely fish, was based on extensive analysis of gut contents. Similarly, Purcell (1992) used gut content analysis to describe the diet of a gelatinous predator (*C. quinquecirrha*). Analysis of gut contents is widely applied in examining the food habits of larger organisms such as fish. Such studies can provide very specific information regarding food habits and may address the sizes and types of prey consumed and how prey choice

varies with an individual's size and age or the season or location of capture (Hartman and Brandt, 1995).

Measures of the relative preference of a consumer for particular diet components are useful for interpreting data from studies of food habits. One such measure is the index of electivity:

$$E_i = \frac{p_i - P_i}{p_i + P_i} \qquad (16.7)$$

where for prey item i, p_i is frequency in the diet and P_i is frequency in the environment (Ivlev, 1961). E_i varies from -1 for an abundant food that is not eaten to $+1$ if the item is much more abundant in the diet than in the environment. The *standardized forage ratio* is another, possibly better, index (Chesson, 1978, 1983). Food preference indices can be useful for evaluating diet composition in food webs. When the diet is unknown, one may estimate it by assuming neutral electivity (i.e., equal preference) for potential prey items. Given independent diet data, electivity can be used to evaluate the data and possibly improve the food web model.

In feeding experiments, another source of diet information for construction of food webs, consumers are presented potential prey items from the natural environment in a tank or enclosure. Selectivity is estimated by examining which items are consumed. Feeding experiments can quantify prey-specific clearance rates for plankton, which are useful in food web models. For example, a large medusa (*C. quinquicir-rha*), can consume all the ctenophores from 2000 l of water each day (Purcell and Cowan, 1995) but can only clear copepods from 48 l of water per day (Purcell, 1992), indicating a preference for ctenophores. Experimental approaches have also been used to examine prey preferences for small zooplankton. For example, plankton dilution experiments, used to infer grazing rates, can use photopigment concentrations to quantify which phytoplankton are grazed (e.g., McManus and Ederington-Cantrell, 1992). Selective grazing has also been measured using instruments that determine numbers and sizes of particles (i.e., flow cytometry; Jochem, 2003).

A variety of chemical markers, including fatty acids and sterols (Bianchi and Canuel, 2011), have been used to study trophic relationships in estuarine food webs. Chemical markers may be passed through one or more trophic transfers, relating presence in a consumer back to a source in the diet. Ideal biomarkers are relatively unique to a particular organic matter source and are transferred with little modification. St. John and Lund (1996) illustrated how the ratio of two fatty acids could indicate the importance of a diatom and a flagellate as the base of the food chain
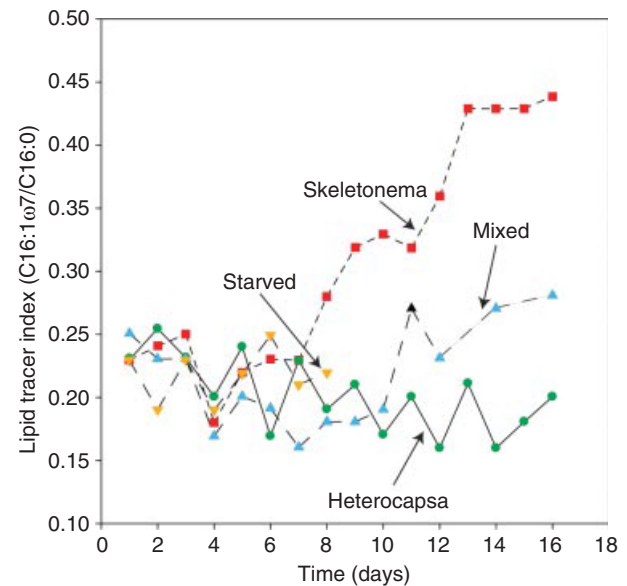
FIGURE 16.12 Results of an experiment following incorporation of lipid biomarkers in a food chain. In each of the three treatments, North Sea cod larvae were fed copepod nauplii hatched from adult copepods raised on (i) the diatom *Skeletonema costatum*, (ii) the flagellate *Heterocapsa triquetra*, or (iii) a 50 : 50 mixture of each. The lipid tracer index is the ratio of abundance in the cod larvae of two specific lipid markers. *Source*: Modified from St. John and Lund (1996).

supporting North Sea cod (*G. morhua*) larvae (Dalsgaard et al., 2003; Fig. 16.12). Copepods were fed one phytoplankton species, and then cod larvae were fed nauplii from each treatment group. The observed fatty acid ratio in the cod larvae resolved the phytoplankton source, even after 2 trophic transfers. Fatty acid and sterol biomarkers have also resolved transfers of organic matter from bacteria to ciliates to copepods, quantifying the significance of the bacterial food source (Ederington et al., 1995). This type of information is particularly useful in combination with other biochemical data, such as stable isotopes.

16.5.6 Stable Isotopes in Estuarine Food Webs

Analysis of stable isotopes of major elements in organic matter can provide information on average food habits and direct, integrative information on trophic position and relative dependence on different types of primary producers. Stable isotopes of carbon (^{12}C, ^{13}C), nitrogen (^{14}N, ^{15}N), and sulfur (^{32}S, ^{34}S) have been widely used in studies of estuarine ecology. Fry (2006) provides an excellent introduction, illustrating both the power of analyzing stable isotopes

and some of the complications inherent in their application to food webs. In a nutshell, the ratio (R) of heavy isotope to the light isotope for a consumer organism reflects that of the organic matter it eats. This relationship is modified by the process of *isotope fractionation*, which occurs because reactions involving the lighter isotope usually proceed slightly faster than those involving the heavier isotope. Isotope ratios are most commonly expressed as a deviation from that of a standard reference material using the double ratio:

$$\delta = \left(\frac{R_{SAMPLE}}{R_{STANDARD}} - 1 \right) \times 1000 \qquad (16.8)$$

where the ratio R is as defined above (Fry, 2006). For stable isotopes of C, N, and S, the elements most commonly used in studies of estuarine food webs, the δ values are $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, respectively, and have units of "per mil" (‰).

Stable isotopes vary across the biosphere in relatively predictable ways (Peterson and Fry, 1987). In the best known examples from estuaries, $\delta^{13}C$ and $\delta^{34}S$ are the most reliable indicators of organic matter sources at the base of the food web. Terrestrially derived organic matter and organic matter from freshwater sources are more depleted of ^{13}C ($\delta^{13}C = -28‰$) than marine phytoplankton ($\delta^{13}C = -21‰$), while seagrasses and marsh plants are least depleted with $\delta^{13}C = -13‰$ to $-10‰$. One complication is that a mixture of carbon from marsh plants (e.g., *Spartina*) and upland plants could have the same $\delta^{13}C$ as marine phytoplankton. This problem can be addressed by simultaneously examining $\delta^{34}S$, which easily differentiates between phytoplankton and the other sources (Fig. 16.13). In the case of the salt marsh at Sapelo Island, the organic matter source for most organisms includes a mixture of plankton and *Spartina* but no significant contribution from upland plants (Peterson and Howarth, 1987).

While $\delta^{13}C$ and $\delta^{34}S$ are the most useful stable isotopes for examining organic matter sources, $\delta^{15}N$ is often useful for characterizing the average trophic position because of the relatively large N isotope fractionation associated with each trophic transfer. Fry (1988) observed that a relatively consistent 3.6‰ increase in $\delta^{15}N$ was associated with an increase of one trophic level (Fig. 16.14). In an example from Fry (1988), planktivorous fish were found to have an average $\delta^{15}N$ of 10‰–11‰, and, based on known feeding habits, were known to have an average trophic level of approximately 3.2. Samples from their plankton diet had an average $\delta^{15}N$ of 6‰–7‰, 4‰ less than the planktivores and reflecting an average difference of just over 1 trophic level. Fry
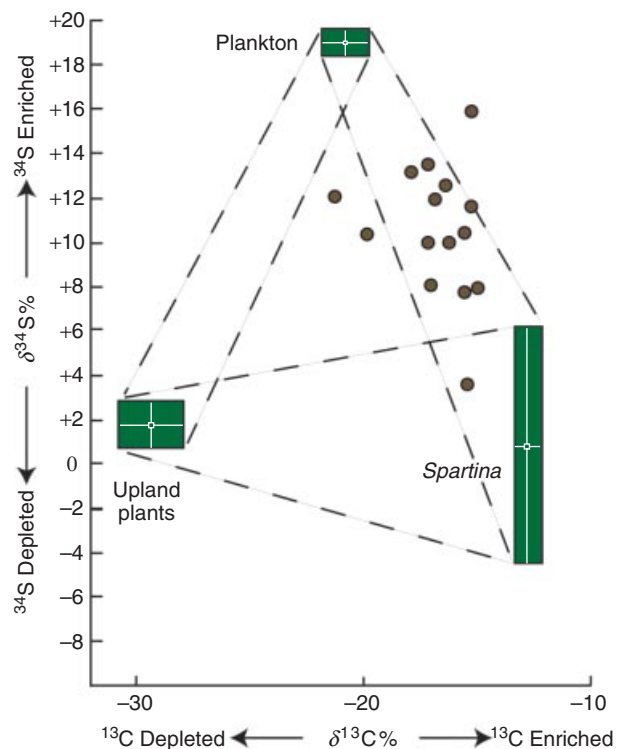
FIGURE 16.13 Graph illustrating the use of stable nitrogen and sulfur data from biota collected near Sapelo Island, Georgia, to evaluate the organic matter sources for the food web. In this case, stable isotope data exclude upland plants as an important source of the food web. *Source*: Redrawn from Peterson and Howarth (1987).

(1988) also observed variable $\delta^{15}N$ for fish characterized as "opportunistic generalists," likely reflecting their varied diet (Fig. 16.14). In another study, Wells et al. (2008) used stable N and C isotopes to explore ontogenetic changes in the feeding ecology, including organic matter sources and average trophic level for red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. The study found an abrupt increase in $\delta^{15}N$ between larval fish and juveniles, followed by a slower increase in $\delta^{15}N$ with age. These results were interpreted to indicate an increase in average trophic level, which was supported by results from analysis of gut contents.

16.6 QUANTITATIVE ANALYSIS OF FOOD WEB NETWORK MODELS

Development of computational methods for analyzing food webs began in earnest in the early 1970s
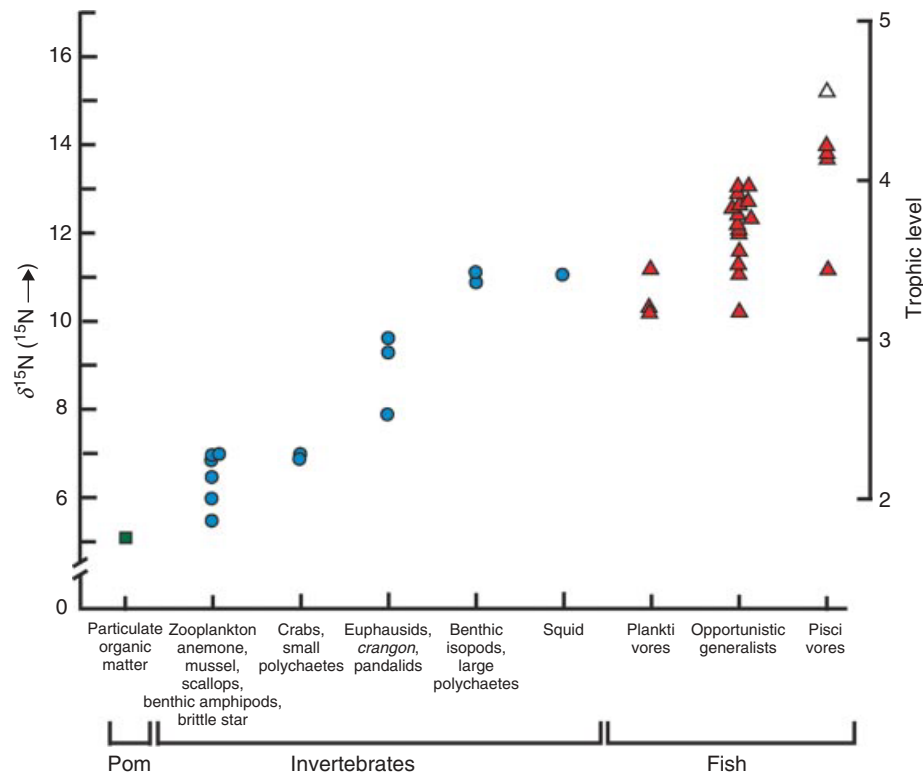
FIGURE 16.14 The relationship between δ^{15}N and trophic level in the food web of Georges Bank. Later research revealed that the ''piscivore'' with particularly low δ^{15}N consumes lower trophic level prey, consistent with the stable isotope results. POM, particulate organic matter. *Source*: Redrawn from Fry (1988).

(Hannon, 1973) with adaptation of Leontief's (1951) economic input–output analysis to analyze ecological networks, rather than economic goods and services. Additional methods developed during the 1970s and 1980s coalesced as *ecological network analysis* (ENA) (Kay et al., 1989). ENA contributed to an evolving quantitative theory of ecosystem development (Ulanowicz, 1986) that was implemented in a computer program called NETWRK and later programs, such as WAND, that added new procedures (Allesina and Bondavalli, 2003, 2004; Ulanowicz, 2004).

Another approach called ''Ecopath'' (Polovina, 1984) emerged independently in the mid-1980s from research on fish ecology of French Frigate Shoals. The main objective was to estimate the biomasses of the coral reef food web components. Ecopath was later expanded to include more sophisticated inverse modeling capabilities and other tools to assist with model construction, and to implement the ENA procedures from NETWRK (Christensen and Pauly, 1992), ultimately becoming ''Ecopath with Ecosim'' (www.ecopath.org; Christensen and Walters, 2004), a comprehensive program for construction, analysis, and dynamic simulation (i.e., simulating changes

over time; see Section 16.6.5) of food webs. Ecopath with Ecosim can implement spatially explicit simulations, which may be useful for examining the spatial mosaic of habitats in estuaries (i.e., as in Section 16.4). Although the software continues to emphasize applications in fish ecology and fisheries management, it can also be applied to other kinds of food webs.

To illustrate quantitative analysis of a trophic network, consider a hypothetical food web with six compartments representing distinct trophic groups (Fig. 16.15). The flows include major trophic pathways that occur in estuaries, including a grazing chain (primary producers, grazers, carnivores) and a detritus-based food web (particulate and dissolved organic matter, detritivores, carnivores). The particulate and dissolved organic matter group includes bacteria as a subcomponent that consumes detritus and generates respiratory losses but returns all the produced biomass back to the detritus pool. Each compartment contributes to detritus as a result of natural mortality and unassimilated food (e.g., egestion). Organic matter inputs include primary production and external inputs of particulate and dissolved organic matter. Exports include particulate

and dissolved organic matter and carnivore biomass associated with fish harvest and emigration.

16.6.1 Mass Balance in Food Web Networks

A fully quantified food web model satisfies several mass balance or ''master'' (Christensen and Walters, 2004) equations. One such equation is the bioenergetic mass balance equation (Eq. 16.1), introduced in Section 1.3, which applies to the aggregate flows to and from a node. A second mass balance accounts for the fate of production (P). The second Ecopath master equation (Christensen and Walters, 2004) balances production for a trophic node with outputs, including catch (i.e., for fisheries), predation losses (i.e., to other nodes), net migration (i.e., immigration minus emigration), and natural mortality. The mass balance also includes a term for the net change in biomass, which applies when food web models consider significant long-term or seasonal changes in biomass. A more generic mass balance equation simply states that, for each node, the sum of external inputs and inflows from other nodes equals the sum of exports, respiration, and flows to other nodes (Ulanowicz, 2004). The Ecopath equations can be related to generic mass balance. For example, the flow from detritivores to carnivores in Figure 16.15 can also be expressed as the product of total predation by carnivores multiplied by the fraction of the carnivore diet obtained from detritivores. Mathematical expressions for the analyses described below are provided by Ulanowicz (1986–1997, 2004) and others (Christensen and Walters, 2004).

16.6.2 Total System Properties

Once a food web has been quantified, ENA can be used to examine *total system properties*, which pertain to the food web as a whole. One question is ''how big is the food web?'' Although it is intuitive to think of ''size'' in terms of biomass, it is often more informative to consider the magnitude of trophic flows. The term *total system throughput* (TST) refers to the sum of all the internal and external flows, including inputs, exports, respirations, and flows among the compartments in the food web. Summing the flows in Figure 16.15, the TST is 2055 g C/m^2/ year (or 5630 mg C/m^2/ day) making this food web fall between the smallest (St. Marks, Florida in January = 1900 mg C/m^2/ day) and the largest (Chesapeake Bay in summer = 1,700,000 mg C/m^2/ day) food webs examined in a comparative study (Christian et al., 2005). TST is usually larger than the sum of the flows into the food web because each unit of input is usually involved in several trophic transfers before being finally lost to the system. The average number of trophic transfers that occur after a unit of material or energy enters the food web is called the *average path length*. The average path length can be computed by subtracting the sum of all inputs from TST and then dividing by the sum of inputs, the result of which is 3.3 for the food web in Figure 16.15.

Another question about total system properties is ''how is the food web organized?'' Drawing from early efforts to quantify species diversity (e.g., MacArthur, 1955), ENA makes it possible to compute *flow diversity* and to decompose flow diversity into two components, *residual diversity/freedom* and *average mutual information* (AMI). AMI quantifies the degree of organization of the flows and is often scaled by TST to compute *network ascendency* or simply *ascendency* (Ulanowicz, 2004). The upper limit for ascendency is called *development capacity* or *capacity*, while the difference between ascendency and capacity is called *overhead*. Ascendency is 30,225 g C/m^2/ year for the example food web in Figure 16.15, which is 37% of development capacity (82,370 g C/m^2/ year), similar to the ratio of ascendency/capacity for many estuarine and other food webs (Christian et al., 2005; Ulanowicz, 2009). Given sufficient data, these quantities can be used to evaluate changes in food webs (Heymans et al., 2007) and to evaluate theories related to ecosystem development (Ulanowicz, 1997, 2009).

16.6.3 Trophic Structure

Quantitative analysis of flows in a food web provides a way to understand the structure of trophic flows, or simply ''trophic structure.'' Flow *cycles*, present in most food webs, involve trophic pathways that return to the trophic node from which they originated. Cycles often involve a nonliving compartment (i.e., detritus, Fig. 16.15). The food web in Figure 16.15 includes seven cycles, five of which involve recycling via detritus. One longer cycle involves five compartments: carnivores → detritus → detritivores → grazers → carnivores. Cycles among living components are relatively rare, perhaps because of the size-based limitations on trophic interactions. However, to illustrate cycles, a flow has been introduced from carnivores to detritivores in Figure 16.15. This could represent a suspension feeding detritivore feeding on an early life stage of a carnivore. This additional flow creates two cycles, one of which is grazers → carnivores → detritivores → grazers. Complex food webs often have many cycles. The importance of cycling can be expressed via the ratio of flows associated with cycling relative to the magnitude of all
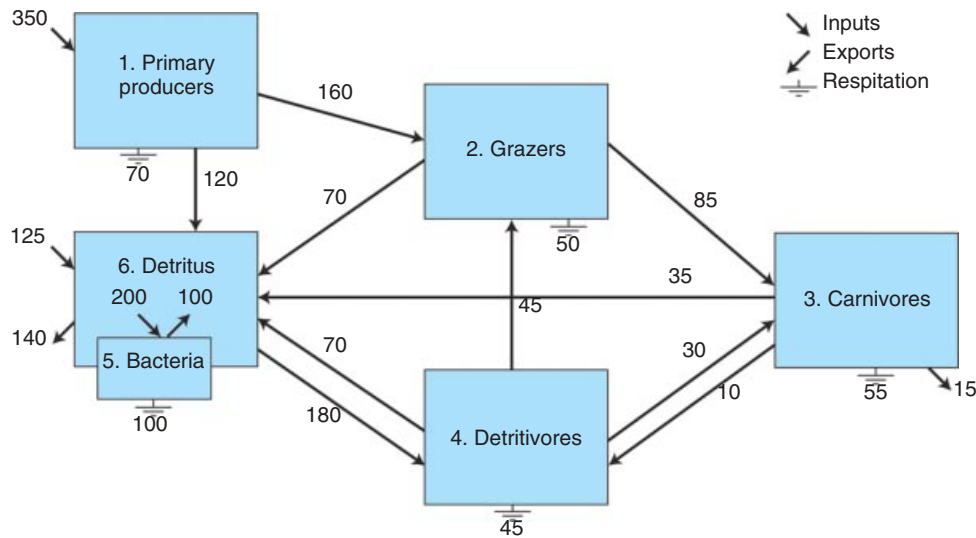
FIGURE 16.15 A simple hypothetical carbon food web for an estuary. Inputs, outputs, respirations, and internal flows have units of grams of carbon per square meter per year. Major components are primary producers (e.g., phytoplankton), grazers (e.g., copepods) feeding on a mixture of phytoplankton and heterotrophic microplankton, carnivores (organisms feeding on zooplankton or small benthic species) and detritivores. Bacteria are represented as a subcomponent of the detritus pool, returning biomass produced back to detritus.

flows (i.e., TST; Finn, 1976). In the example food web, the sum of flows due to cycling is 535 g C/m^2/ year, which amounts to 28% of TST.

As indicated earlier (Section 16.2.2), complex food webs can be represented as an "effective food chain" composed of virtual or "canonical" trophic levels (Fig. 16.6) by apportioning the network of flows among a series of integer trophic levels (Ulanowicz and Kemp, 1979). This representation, sometimes called a "Lindeman trophic aggregation" or "Lindeman spine," can provide insight into trophic structure. A key step involves mathematically removing flows associated with cycles among living compartments, as these create, in theory, an infinite number of trophic levels. Cycles involving detritus may remain since by convention the trophic level of detritus is equal to 1 (i.e., primary producer). The effective food chain generated from the food web in Figure 16.15 has four virtual trophic levels (Fig. 16.16). The longest path begins with either primary producers or detritus and involves flow from detritus, to detritivores, to grazers, and then to carnivores (i.e., 6 → 4 → 2 → 3; Fig. 16.15). Only a small fraction (13%) of consumption by carnivores occurs via this pathway. As a result, the yield to humans of carnivores is at an average trophic level of only 3.16, or 16% at trophic level 4 and 84% at trophic level 3. This is typical of the world's fisheries harvests (Pauly et al., 1998).

The effective food chain may also describe average efficiency of the food web at each virtual trophic
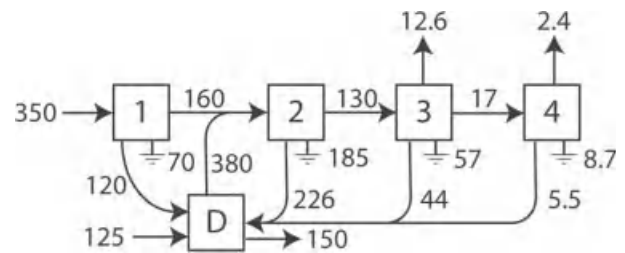
FIGURE 16.16 The effective food chain obtained by projecting the food web in Fig. 16.15 into a chain of "canonical trophic levels." Flows to detritus are collected in a detritus compartment (labeled "D") and assigned a trophic level of 1. Exports from trophic level 3 and 4 total to 15, the export from compartment 3 (carnivores), revealing the "apportionment" of activity between trophic level 3 and 4. The effective trophic level for carnivores is 3.13 because most of the export is at trophic level 3.

level. Of the 750 g C/m^2/ year input to trophic level 1 (phytoplankton plus detritus), 540 g C/m^2/ year, or 72%, flows to the second trophic level (Fig. 16.16). Upper trophic levels tend to be less efficient. In Figure 16.16, only 24% of the flow to trophic level 2 is passed to the third trophic level and only 13% is subsequently passed to the fourth. The highest trophic level has, by definition, a trophic efficiency of zero.

16.6.4 Indirect Interactions

Analysis of food web models enables quantification of how flows depend on any other flows, whether

directly or indirectly (Ulanowicz, 2004). For example, an important question is how much the flows within the food web ultimately depend on a specific input, such as primary production. Inputs in the example food web (Fig. 16.15) include primary production and detritus. Network analysis reveals that 84% of the export from compartment 3 depends on primary production, even though there are no flows from primary producers to compartment 3. The *total dependency matrix* (Szyrmer and Ulanowicz, 1987) generalizes this kind of analysis, quantifying the fraction of each flow that previously flowed through each of the other nodes via all pathways. A related concept is the *total contribution matrix*, which quantifies the fraction of flow from each node that eventually reaches each of the other nodes, again via all pathways. As an example, the total contribution matrix for the example food web (Fig. 16.15) indicates that 50% of phytoplankton production reaches grazers via all pathways, even though only 46% of primary production flows directly from primary producers to grazers. The contribution matrix is related to the concept of *primary production required* (PPR, Christensen et al., 2004), which illustrates the magnitude of PPR to sustain a particular fisheries yield. In the example, 26% of the primary production flows to carnivores via all pathways. Thus, 90 g $C/m^2/$ year of primary production is required to sustain the harvest of carnivores.

A useful way to understand both direct and indirect trophic impacts in a food web is to use a procedure called *mixed trophic impacts* (Ulanowicz and Puccia, 1990), which expresses the net effect of a node on another node via a coefficient between -1 (strong negative effect) and $+1$ (strong positive effect). For example, the direct effect of primary producers on grazers (Fig. 16.15) is strongly positive ($+0.78$) and the net effect of grazers on phytoplankton is, not surprisingly, strongly negative (-0.57). Carnivores have no direct effect on phytoplankton; their indirect trophic impact is positive ($+0.17$) because they exert top-down control on the grazers, implying a subtle trophic cascade (Section 16.3.4).

16.6.5 Dynamic Simulation of Food Webs

Thus far, all the food web models that have been discussed are *static* models. That is, they describe the magnitude of trophic flows in a food web as either observed or calculated (e.g., via inverse analysis). Although much can be inferred from static food web models, particularly by comparing models for different times and places, they cannot address ''what if'' questions. For example, ''how would the food web change if an important predator or grazer

were eliminated?'' Another question might be ''how would the food web change if an important habitat was made unavailable?'' These questions can be addressed using *dynamic* food web models, which simulate changes in biomass and flows through time. Although dynamic simulation models are not new, successful applications to complex food webs are relatively new. One problem that has been encountered is that dynamic food web models tended to ''self-simplify,'' unrealistically losing trophic groups (i.e., their biomass goes to zero), whereas real food webs tend to maintain diversity (Walters et al., 1997). To address this, Walters et al. (1997) observed that predator–prey encounters can be mediated by behavioral or physical mechanisms that can limit the availability of prey. A model structure representing these processes performed much better and incorporated as ''Ecosim'' into the previously mentioned Ecopath with Ecosim software. The software has since been generalized by adding ''Ecospace'' to support spatially explicit simulations, broadening the range of the ''what if'' questions that may be addressed (Pauly et al., 2000). Dynamic food web models require all the information needed to quantify static food web models, plus additional information to characterize trophic dynamics (e.g., how flows change in relation to changes in biomasses of each trophic node). The additional data requirements for parameterizing dynamic food web models poses a challenge for ensuring that these models are well constrained by data.

16.7 APPLICATIONS OF FOOD WEB ANALYSIS IN ESTUARIES

Analysis of estuarine food webs from a holistic perspective is valuable for several reasons. Analysis of estuarine food webs as a whole is useful and necessary because estuarine ecosystems function as an interactive whole and cannot be fully understood by examining only a subset of the whole. Analysis of estuarine food webs can help in identifying errors or gaps in our ecological understanding. This is important because quantifying estuarine food webs usually involves assembling many different kinds of information. Uncertainty is reduced by reconciling independent observations via the mass balance and other constraints associated with quantifying food webs (Section 16.6.1; Christensen and Walters, 2004; Ulanowicz 2004). Quantifying the whole may also reveal if one or more components has been overlooked or mischaracterized (Guénette et al., 2008). In this sense, analysis of whole food webs is useful in the

same way as construction of estuarine nutrient budgets, which interrelate independent measurements of nutrient inputs, fluxes, and transformations via a mass balance (Chapter 17).

Analyzing estuarine food webs makes it possible to contrast food webs and characterize changes over time. These changes may then be related to factors causing the change. Food web changes may be reflected in total systems properties, such as total systems throughput or average path length, or, alternatively, in properties that pertain to one or more nodes, such as average trophic level of a species or of the total fisheries harvest (Christian et al., 2005; Shannon et al., 2009). Such changes can be caused by a variety of factors, including eutrophication (Baird et al., 2004) and fishing pressure (Breitburg et al., 2009), both potentially important in estuaries. Major storms and river flow events may also impact food webs. Although studies have characterized the effects of such perturbations on components of estuarine food webs (Paerl et al., 2006), more holistic analyses appear to be lacking. In general, understanding and predicting how many of the factors that impact estuaries (e.g., river flow, nutrient loading, storms, habitat modifications, climate change) impact the size, structure, and function of whole food webs remains a fertile ground for research.

Food web models can be used to optimize design of ecological interventions such as restoration projects and marine protected areas. For example, a food web analysis showed that creating a small marine protected area can actually increase rather than decrease the catch of top predators because of trophic cascades (Walters et al., 2000). Food web models were also used to quantify the increase in fisheries production associated with a marsh restoration project on Delaware Bay (Frisk et al., 2011), to evaluate the impact of a marine reserve in St. Lucia on nearby artisanal (i.e., small-scale) fisheries and to understand how a wildlife refuge in Florida benefited nearby recreational fisheries (Roberts et al., 2001). A good goal would be to develop estuarine food web models paired with field-based and experimental research programs that can be used to both support modeling and test the conclusions that may be drawn from them.

Analysis of estuarine food webs is a useful tool for environmental management, particularly as management moves from single species to ecosystem-based management (Dame and Christian, 2006). In fact, the US National Oceanic and Atmospheric Administration (NOAA) recognized the development of ECOPATH as one of the top 10 scientific breakthroughs in the 200-year history of the agency (including its predecessor, the US Coast and Geodetic Survey, founded in 1807). Nonetheless, much potential remains unrealized. Environmental management programs often aim to achieve, maintain, or maximize things such as ecological integrity or condition, biological productivity, and ecological services (e.g., Borja et al., 2009). Yet, these concepts often lack adequate operational definitions, particularly in estuaries. Practical approaches for monitoring, assessing, or goal setting are often lacking. Tools for linking management of water quality and food webs are still in their infancy (Cerco et al., 2010). Faced with inadequate data and tools, management of estuarine ecosystems must sometimes fall back on simpler indicators such as chlorophyll *a* concentration (e.g., Boyer et al., 2009), which do not capture important aspects of ecosystem integrity, condition, or services. Building on the worthy foundation that already exists, there remains a real need to develop practical scientific methods and tools to enable policy makers to quantify and relate water quality and habitat quality in estuaries to meaningful indicators of estuarine food web structure, function, and condition.

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BUDGET ANALYSES OF ESTUARINE ECOSYSTEMS

Walter R. Boynton and Scott W. Nixon

*Give me but one firm spot on which
to stand, and I will move the earth.
Archimedes (Oxford, 1953).*

17.1 INTRODUCTION

Present-day ecologists can sympathize with Archimedes, the ancient Greek mathematician and engineer often credited with the invention of the lever, a very simple but powerful machine. Our ambitions are more modest than his, but we, too, are much in need of some firm ground on which to stand. As previous chapters in this book have shown, estuaries and other coastal ecosystems are very complex mixes of social and natural systems that are highly variable on many scales of space and time. Much of our knowledge is based on imperfect measurements made on individual pieces of ecosystems—chemical concentrations, current speeds, cell counts, fish landings, and the like. Also, we are finding new pieces and new connections among the pieces all the time. In the face of such great complexity, variability, and uncertainty, how do ecologists step back and check to see if the various pieces are fitting together, to see if they are missing important pieces, to see if their measurements are making sense? One of the most important tools we

use is, like the lever, very simple in concept but very powerful in its application—the budget.

In its simplest form, a budget for an organism, a population, an ecosystem, or the biosphere is just what it is for a person, a family, or a country—a balancing of what comes in, what goes out, and how much has changed within the system during the time period of interest. A major difference is that most human beings are usually interested in budgeting money rather than things such as energy, water, carbon (C), nitrogen (N), phosphorus (P), sediment, or various pollutants such as heavy metals that are usually the subject of budgets that coastal and estuarine ecologists make. Another important difference is that ecosystems cannot create energy or materials like governments can print money nor can ecosystems borrow from the future. In other words, ecosystems are constrained by the firm ground of the laws of conservation of mass and energy. Any difference between what comes in and what goes out must be accounted for by a decrease or increase in the amount the system started with. Thus, there must be over any time period a mass or energy balance of these three terms

or components of the budget—inputs, outputs, and changes in storage. This constraint is the ''firm spot'' on which all our ignorance, errors, and uncertainty must come to rest and be resolved or, at the very least, recognized.

17.1.1 Making Budgets

Constructing budgets (mass or energy balances) at whatever level of organization, from individuals to ecosystems, is often as challenging in execution as it is simple in concept. It usually involves a synthesis of many different kinds of measurements made by many different people in many different ways and at many different times to generate the holistic picture of a budget. And the picture that results may be exciting and rewarding (Wow -it all makes sense!) or humbling and frustrating (What are we missing? Those data must be wrong!).

Ecologists (and managers) also often want to go beyond first-order accounting of inputs, outputs, and changes in storage of a total element to ask about the different forms of material or energy. For example, it complicates the task greatly to try to budget not just total N but all the constituent forms of N—ammonium (NH_4), nitrite (NO_2), and nitrate (NO_3)—which together constitute dissolved inorganic N or DIN; N_2 and N_2O gases (which are inorganic forms of N that can be dissolved in the water but are not included in traditional DIN); dissolved organic N or DON (which is itself a complex mix of compounds); and particulate organic N or PON (which ranges from viruses and bacteria to whales). Of course, accounting for some or all of the different forms allows us to learn much more about the organisms and processes that are producing the overall changes in N that we see in the total N budget.

Many efforts to develop budgets also grow more complicated because they include processes that contribute to the overall behavior of the budget. For the example of an N budget, we can ask questions like, ''Once DIN enters the estuary, how much is taken up by the phytoplankton compared to the macroalgae? How fast does N in plankton and macroalgae get recycled into DIN before it is lost from the system?'' Such questions may be important and answering them may lead to new knowledge. However, they may also distract us from the task of completing an ecosystem level mass balance. As more detail is added to the budget, more questions will likely arise about how those details may change over time or under different environmental conditions. Trying to answer these questions requires that the budget becomes dynamic rather than remain static. In this way, a static budget can evolve into a dynamic simulation model.

Such dynamic models must also maintain a mass balance for all constituents they simulate—from salt and water to C, N, and P—and this can be a very demanding standard. No matter how mathematically elegant or rich in detail models become, no matter how colorful and impressive their GIS-based output becomes, they rest on the base of the humble budget.

17.1.2 A Brief History of Budgets in Coastal Ecology

The budget is such an intuitive concept that it has been part of our thinking about nature for a very long time. Its use as a formal scientific framework for studying ecosystems seems to have begun in the late 1800s and early 1900s. Hutchinson's (1957) classic *Treatise on Limnology* describes the first (and flawed) heat budget for a lake published in 1880 and the development of water balances for watersheds and lakes beginning in the early 1900s but did not discuss nutrient budgets explicitly. It seems likely that the rising awareness of nutrient pollution as a serious problem in lakes stimulated the development of nutrient mass balances by freshwater ecologists beginning in the 1960s (National Academy of Sciences, 1969). The development of nutrient budgets for marine ecosystems can be traced to the much earlier work of Johnstone (1908) who estimated and/or identified many of the terms of the N budget for the North Sea. He reported that far more N flowed into the sea from land than was returned in fisheries landings. This balance is still of interest for estuaries (Deegan, 1993). The more recent concerns with nutrient pollution in coastal marine systems led to the development of nutrient budgets for many estuaries (Smith and Atkinson, 1994; Boynton et al., 1995; Nixon et al., 1995) and even continental shelf systems (Nixon et al., 1996). Nutrient pollution aside, budgets can tell us other important things about coastal ecosystems, including their net ecosystem metabolism (do they produce more organic matter than they consume?) and export of primary and secondary production to other systems (Nixon and Pilson, 1984; Kemp et al., 1997). Such basic ecological questions, as well as the link between nutrient pollution and eutrophication, stimulated a large international effort to develop nutrient budgets for many estuaries using a standard methodology. More details of the ambitious project, Land-Ocean Interactions in the Coastal Zone (LOICZ) can be found in the Web site http://www.loicz.org/products/budget/index.html.

While water and heat energy budgets appear to be more common in lakes, the approach has been applied to coastal marine ecosystems including lagoons (e.g., Smith, 1994) and salt marsh tidal creeks

(McKay and Di Iorio, 2008). Mechanical energy budgets are more common in the much more energetic tidal systems of the coasts and continental shelves (Nixon, 1988, see also Taylor, 1919 for the Irish Sea and Foreman et al., 2006 for the Bering Sea). Examples of mechanical energy budgets involving wind and tide in smaller estuarine systems include Narragansett Bay, RI (Levine and Kenyon, 1975), Great Bay, NH (Brown and Trask, 1980), and Long Island Sound, NY (Bokuniewicz and Gordon, 1980). As we noted earlier, any estuary where credible models of water circulation and ecosystem dynamics have been developed also has budgets embedded in those models of water, salt, perhaps heat, mechanical energy, and biogenic elements that are simulated (C, N, and P).

Sediment budgets have documented the ''aging'' or filling in of estuaries and the importance of major storms on sediment delivery (e.g., Schubel and Carter, 1977; McKee et al., 2006). With the growing awareness of environmental pollution in the late 1960s and 1970s, geochemists linked sediment budgets with a variety of pollutants to develop budgets of heavy metals, nuclides, and petroleum hydrocarbons in coastal systems (Turekian et al., 1980; Nixon et al., 1986; Marcus et al., 1993). Such budgets play an important role in helping to identify the relative importance of various sources of pollutants and suggesting priorities for remediation and treatment. They also highlight important sinks for different pollutants and pathways by which they may be transported to adjoining systems.

In the remainder of the chapter, we give examples of case studies illustrating estuarine budgets of varying purpose and complexity that have been prepared and analyzed in different ways. First, we discuss budget definitions, boundary setting, the choice of units, and issues of uncertainty and error (Box 17.1). We then present a selected number of budget case studies and close with examples of the application of budget analyses in environmental management issues.

17.2 PRINCIPLES AND METHODS

17.2.1 Definitions

Simply put, budget analyses or mass balances are an application of the conservation of mass or energy laws to physical (e.g., water and salt balances), chemical (nutrient budgets), or biological (e.g., salt marsh) systems, communities, or individuals. The constraint that mass and energy must be conserved is the foundation of budget analysis. Budgets that balance

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> **BOX 17.1   Budget Terms**
>
> There are a number of terms that ecologists, biogeochemists and others who make budgets use frequently. Some of them are defined below:
>
> SYSTEM – the entity for which a budget is being made. The system can be at any level of organization and it may be living, non living, or a mix of both.
>
> TIME OF REFERENCE – the time period over which the budget is being developed, usually a day, a season, or a year in ecological work.
>
> BOUNDARY – the physical perimeter of the system, including the depth of soil or sediment.
>
> INPUTS – energy or material that crosses the boundary from outside the system.
>
> OUTPUTS – energy or material that crosses the boundary from inside the system.
>
> SOURCES – where the inputs come from or, in some cases, the processes that generate the inputs (e.g. N fixation is a source of N).
>
> SINKS – where the outputs go or the processes that generate the outputs (e.g. denitrification is a sink for N) or places in the system where the energy or material being budgeted accumulates without participating in processing within the system. For example, long term burial in sediments may be called a sink for some pollutants that adhere strongly to particles.
>
> TRANSFORMATIONS – are changes in the form of the material being budgeted within the system (e.g. dissolved N may be transformed into particulate N).
>
> RESERVOIR – a place where the material being budgeted accumulates or is stored within the system.

(inputs = outputs + changes in storage) lead us to believe that we have some understanding of the system while those that do not balance indicate that we have missed something important.

The *conservation of mass/matter* states that the mass of a closed system will remain constant; matter can be neither created nor destroyed although it can be rearranged. This implies that for any process in a closed system the mass of the reactants must equal the mass of the products. In common-sense wording, all inputs of matter must be accounted for in storages or outflows of matter.

The *conservation of energy* law states that the total amount of energy in an isolated system remains constant but can change from one form of energy to another (e.g., kinetic to thermal). In common-sense wording, all the energy that enters a system is either stored there or flows out.

In simple terms, most mass or energy balances used in estuarine studies take the form of accounting for all known inputs, outputs, and changes in the amount of mass or energy in the system (i.e., increase in stored carbon due to growth). However, as a practical matter, many ecosystem-scale budgets assume steady-state conditions where there is no net change in storage for the period of time considered in the budget.

During the past few decades, it has become abundantly clear that many estuarine environments are seriously degraded and this has spawned a variety of studies designed to assess environmental conditions, detect trends, and serve as a basis for implementing pollution control measures. As a result, large amounts of data have become available for many estuarine systems. However, much of this information has been interpreted in terms of relatively narrow issues (e.g., have nutrient and chlorophyll concentrations changed? Have hypoxic zones increased in size?). From these sources, it is difficult to gain an understanding of the relative importance of various inputs, losses, transformations, and transport of materials. The construction and evaluation of budgets provides a conceptual and practical framework to gain perspective and understanding of these issues.

17.2.2 A Simple Example . . . Was Dave a Drinker?

Dave, our first example of using budgets to answer interesting questions, was not an overenthusiastic consumer of red wine or summer ale but was a California sea lion, *Zalophus californianus*. And the liquid in question was seawater. The question is interesting because sea lions live on dry rocky islands where there is no fresh water. They eat large amounts of fish and squid high in protein and thus nitrogen (N). Metabolizing the protein produces toxic N compounds that must be excreted in urine. In the mid-1960s, a young biochemist named M. E. Q. Pilson working at the San Diego zoo began asking himself how sea lions obtained the water they used to produce urine and excrete the N. Did they drink sea water? If so, they had another problem—they would have to excrete the salts that the water contained. This was also a problem with the squid in their diets since these contain high concentrations of salt. Could the animals obtain enough water from the fish flesh and metabolize the organic matter it contained? Recall that respiring organic matter produces water as well as carbon dioxide. Dr. Pilson decided to answer his question by making budgets.

Working at a zoo had certain advantages, including access to the young sea lion named Dave and a "metabolic cage" in which Dave could be maintained and his food intake carefully monitored for water, N, and salts. His urine and fecal waste were also collected each day and their contents measured. Pilson (1970) presented Dave's total input and output of water, N, and salts for a forty-day period during which Dave neither gained nor lost weight. His daily average consumption of 1.6 kg of mackerel kept him in steady state at 50-kg body mass. The author also noted, "The most important result is that Dave survived the entire period without apparent ill effect." But Dave also answered his question and provided some introductory lessons about budgets (Fig. 17.1).

The beauty of Dave's budgets is that the boundaries of the system are obvious, unambiguous, and unchanging—his body. A second nice circumstance is that the internal storages did not change—he was in a steady state of weight so we can *assume* that the amount of water, N, and salt he contained did not change over the 40 days. Inspecting the N budget shows immediately that urine is by far the most
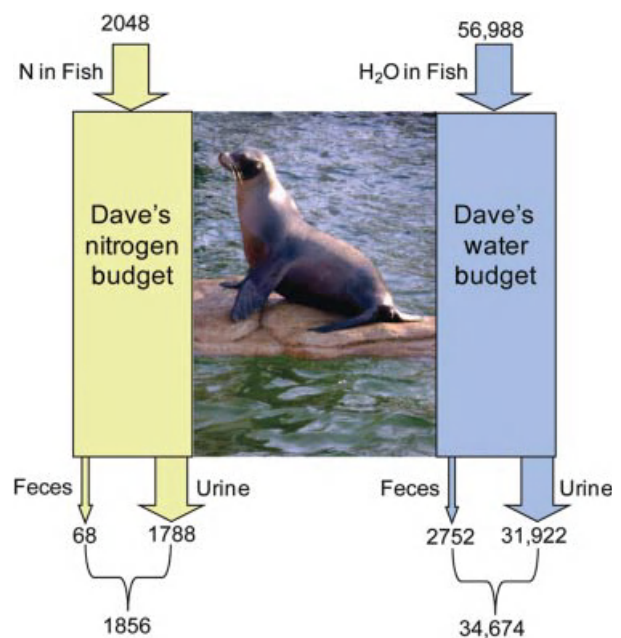
FIGURE 17.1 A simple nitrogen and water balance for "Dave the Sea Lion." Both nitrogen and water flows are in units of grams per 40 days. See text for details of this budget development. *Source:* Data are from Pilson (1970).

important path by which N was removed and that the measured total output of N is very close to the *estimated* input. We say estimated input because the N content of each fish fed to Dave could not be measured and there is some variation in N content of individual fish. A mean N content per unit weight of mackerel was used to calculate the total N consumed. A more important point is that while the input and output of N is close, almost 10% of the N input was not accounted for even under these tightly controlled conditions in a simple system with clear boundaries, daily measurements, and a meticulous, highly trained analyst. The water budget is even more out of balance with total measured output only equal to 61% of the input. Over 80% of the input was ''preformed'' water in fish flesh and, again, urine is by far the major loss term. The ''missing'' water loss amounted to more than 22 l that Pilson (1970) attributed to evaporation from Dave, largely in his exhaled breath. An important lesson is that even simple systems may not be as well constrained as we first think them to be. But even with these problems, the answer to the question that prompted the budgets seems clear—Dave survived and handled his N balance well without the need to consume any water other than that contained in the fish he consumed. Neither he nor other sea lions need drink seawater to survive.

17.2.3 Deciding on Space and Timescales for Mass or Energy Budgets

There are a few hard and fast rules concerning the boundaries of a budget. Mass and energy balances have been carried out for systems as large as the continental shelf of the North Atlantic Ocean down to the size scale of individual organisms. However, as a practical matter, boundaries are often chosen based on common-sense ideas. In many instances, whole system evaluations of nutrient, contaminant, or organic carbon budgets use the physical shape of an estuary as a boundary. In many of these cases, a river is at the head of the estuary (the upstream boundary), shorelines define the sides, and the ocean is the seaward boundary. In other cases, the morphology of the estuary is employed in defining boundaries. For example, N and P budgets for the entire Baltic system were divided into seven subbasins based not only on both shoreline geography but also on the location of subsurface sills and associated deep basins (Savchuk, 2005). Boundaries for nutrient budgets for Chesapeake Bay and tributary rivers were based on these considerations (Boynton et al., 1995). In other cases, boundary determinations are not quite as simple. For example, sea grass beds have edges but these are often not as sharp as a shoreline; there are often

large areas of dense vegetation but then less dense areas, particularly at the edges of the bed. In some of these cases, budgets are developed for unit areas (rates or mass per square meter) representing the dense, well-developed portion of the bed (Risgaard-Petersen et al., 1998). Similar uncertain edges occur in tidal marsh systems having both vegetated areas and areas of intertidal bare sediments and tidal creeks. For any budget, it needs to be clearly stated where the boundaries are located.

A general principle for selecting boundaries involves the notion of feedbacks. In all living systems, feedbacks are essential control mechanisms. For example, in a planktonic system, unicellular autotrophs use light energy to produce organic matter from inorganic carbon and nutrients. Zooplankters then not only consume the plankton as a food supply for maintenance, reproduction, and growth but also provide ''feedback services'' in the form of nutrient recycling, selective feeding on phytoplankton, and the like. Basically, these components are coupled by pathways of food production and feedbacks. In general, boundaries should be drawn where flow pathways of materials or energy are unidirectional and where feedbacks are either weak or basically nonexistent. In the case of an estuarine nutrient budget, inputs to an estuary from a river are largely unidirectional; with the interesting exception of anadromous fish migrations (Krokhin, 1975 for salmon and Durbin et al., 1979 for the alewife), there are no significant feedbacks from the estuary to the upland sources of nutrients.

Selection of budget timescales is also often based on common sense. Timescales need to be consistent with the dominant processes examined in the budget. For example, in bioenergetic budgets of fishes, species timescales of decades would exceed the lifetimes of many fish species; these models are generally evaluated on timescales of hours and days. Conversely, an estuarine organic carbon budget is often evaluated based on measurements made at the daily timescale and then scaled up to seasonal and annual time periods. Finally, data availability often impacts development of budgets. For example, in temperate zone estuaries, there are periods of high and low production and respiration that vary with seasonal patterns of temperature, river flow, nutrient availability, and other factors. Given this, seasonal budgets are often particularly useful. However, in many cases, data may not be available for such finer-scale computations. So, in some instances, the temporal resolution of a budget is governed simply by data availability.

17.2.4 Scaling Measurements to Budget Requirements

Mass and energy budgets are basically empirical exercises, that is, they are based on measurements made in the environment. Many researchers have stood on the deck of a research vessel, groped around in the jungle of salt marsh vegetation or examined data from a pile of publications, and asked a question central to constructing budgets. That basic question is ''how representative is this sample?'' Does it represent just this bucket of water, or the mid-salinity zone of the estuary or conditions in the full estuary?

However, there are some techniques available to help scale-up measurements necessarily made at small scales to the larger scales generally needed in budget development. Schneider (1994) provided a series of practical strategies (with strengths and weaknesses) for scaling up environmental data. These include (i) simple multiplication of small-scale measurements to the size of the natural system; (ii) use of such linear scaling only for those quantities that have limited scope values (ratio of the largest to smallest value); (iii) use of large extent, fine-grain data (e.g., large-scale and fine-grain ocean or terrestrial color images) coupled with small timescale and space scale measurements (e.g., field-based algal biomass estimates) to obtain large-scale estimates via summation rather than multiplication and several other more complex techniques. Here, space precludes providing examples of each of these techniques, but Schneider (1994) provides several examples of each approach. Typically, scaling up of environmental data used in estuarine budgets has used the three approaches listed above or some combination of these approaches.

17.2.5 Mass Balance versus Simulation Models

Those just beginning to understand and use mass and energy balance models often ask about the differences between these and simulation models. Furthermore, there are questions concerning the strengths and weaknesses of these analytical techniques. The basic answer to the first question is that both mass balance and simulation models start with a conceptual model and require quantitative evaluation of inputs, internal losses, storages, and exports. In short, both must meet the criteria of mass or energy balance. However, in the case of mass balance models, the task is completed when all flows (and storages when needed) in the conceptual model are evaluated and explained. In contrast, simulation models also require explicit mathematical formulation of the mechanistic

relationships of flows and interactions of flows and storages (also called *state variables*). For example, in an organic matter mass balance budget, it is sufficient to know the rate of organic matter production, whereas in a simulation model, the relationships between sunlight, nutrients, grazing losses, and other factors must be estimated and formulated into a mathematical expression estimating the rate of organic matter production. So, mass balance requires a value; simulation requires both a value and a mathematical explanation of the value. Thus, simulation models require more data than do mass balances and also more understanding of system components and interactions among components. Simulation models are more difficult to develop but, because they are run forward through time, allow for prediction or forecasting and are often used for this purpose.

17.2.6 Dealing with Errors in Mass and Energy Balance Models

One certainty in science it is that there are errors in all measurements and analyses. Mass and energy balances are, despite the simplicity of the concept, no exception. This section considers a few ways error can be evaluated in budgets and a few ways large errors can be avoided.

17.2.6.1 Some Simple Error Evaluations

Estimates of measurement error can readily be developed for many variables. For example, instruments have levels of detection and various levels of precision. Laboratory analyses of many variables can be conducted with a high degree of accuracy and precision. Even more complex processes, such as rates of algal production, denitrification, or sediment remineralization of organic matter, have errors that can be evaluated by taking replicated samples and computing measures of variance. In all of these examples, quantitative estimates of error can be generated.

At larger scales, there may be monitoring programs, as, for example, by the US Geological Survey (USGS, 2004; http://va.water.usgs.gov/chesbay /RIMP/loads.html), that measure such parameters as river flow, nitrogen and phosphorus concentrations, rainfall, and other weather data, and these data have error estimates associated with them. However, not all inputs to estuaries can be measured, and error evaluated, so directly. Landscape models have frequently been used to estimate inputs and associated errors. For example, Williams et al. (2006) used a watershed model to estimate inputs from nongauged portions of the Patuxent River estuary and reported annual-scale errors for flow, TN, and TP inputs of 26%, 15%, and 40%, respectively, and

also found that model errors declined from short (<1 day) to long (multiyear) timescales because over- and underestimates of flow and load tended to cancel out.

However, this still leaves us with the question of just how good a mass balance evaluation might be. Are the errors likely to be so large that conclusions are hard to reach or are compromised? Investigators have used some simple approaches that provide an indication of uncertainty in budget results and the first relies on the budget framework itself. Budgets require all inputs, changes in storages, and losses to be identified and quantified. The simple comparison of the magnitude of a variety of inputs or losses serves as a check on these values. If an input or loss term in a budget is much larger or smaller than anticipated, then data sources and calculations should be checked. Some investigators have used the idea of a range of values for budget terms where such estimates are available. For example, Nixon et al. (1995, 1996) used this approach in developing nutrient budgets for a variety of estuarine systems. It appears that in most cases the range of values was not large enough to change budget conclusions but does remind us that even simple budgets need to be checked. Finally, it is important to remember that many mass or energy budgets are not complete evaluations. In these cases, one term of the balance is estimated by subtraction of all known losses from all inputs. For example, net exchanges of nitrogen and phosphorus between Chesapeake Bay and the coastal ocean were determined in this manner because it was simply too difficult to directly estimate these values (Boynton et al., 1995).

17.2.6.2 Avoiding Big Errors

Avoidance of ''big errors'' in budget analyses is of central importance. By big errors we mean the type of error that would change, in an important manner, the results of a budget analysis. This sort of error is much larger than the error associated with a chemical analysis or a measurement of temperature.

For example, measurements essential for budgets are often made on a small size scale (e.g., sediment oxygen consumption or sediment denitrification using an incubation chamber covering 0.25 m^2 of sediments). One common feature of many measurements is the need to ''scale-up'' these measurements in both time and space and herein lies one of the possibilities for making big errors. Have sufficient measurements been made in time and space to allow for an accurate estimate of these processes at the full scale of the system being examined? Much of the time these measurements, most of which are complicated, are limited by resources needed to

make these measurements; in general, it is likely that these processes have been undersampled.

So, what are the options for avoiding big errors arising from scaling-up limited measurements of key processes? Approaches include (i) use of literature sources, (ii) ''back of the envelope'' range-finding estimates, and (iii) independent estimates based on alternative methods. Just a decade ago, many of the rate processes needed to develop budgets were scarce and some methodologies still in developmental stages. The literature is now a rich source of data for making comparisons. For example, there are many estimates from estuaries of denitrification and sedimentation rates (Boynton and Kemp, 2008), and the many rates used in fish bioenergetic models have been evaluated for many species (Niklitschek and Secor, 2005). So, one method for avoiding big errors is to consult the literature. Are values measured for a budget within the range of those reported in the literature? If not, is there sufficient reason to use them or do they need to be reevaluated or augmented with additional measurements?

An additional tool for estimating error is back of the envelope calculations. This is a simple ''first-order'' estimation based on whatever information is readily at hand (and hence the name); it can provide a rough estimate of the magnitude of a process and a quick check to see if a budget makes sense. For example, one of the most difficult to quantify terms in estuarine budgets is the input of groundwater and the dissolved materials (such as nitrate) that it carries. Groundwater is out of sight and moves at varying rates through different types of substrate (sediments and rocks) so that measuring the total flow is very difficult. One promising new technique is the use of various naturally occurring radioactive isotopes (e.g., ^{226}Ra; Moore, 1996). In one application of this approach to a coastal lagoon, the first results suggested that there was a surprisingly large input of groundwater that greatly exceeded surface stream flow. This was an exciting finding that had major management implications regarding the importance of individual septic systems as nitrogen sources for the lagoon—even though nitrate concentrations in the groundwater were relatively low, a large flux of groundwater would be adding a large amount of nitrate. The radiochemistry seemed solid and the complex data analysis was intimidating—until a skeptic's back of the envelope calculation showed that when added to the well-known surface water inflow and the loss of water in evapotranspiration, the estimated groundwater flow would require more than three times the annual rainfall on the watershed.

Oops! Subsequent work showed that the concentrations of radioisotopes in the groundwater were much more variable than had been assumed. While the new approach could be powerful, it would not be as easy as it first seemed. The moral of the story is that in developing budgets (as in so many things), keeping it simple can often keep us from going astray.

Finally, the use of alternative methods for computing rates can confirm results obtained using a primary methodology or indicate a substantial problem exists. For example, Boynton et al. (2008) used several different approaches of determining sediment input to the Patuxent River estuary and showed that sediment inputs were sufficient to support measured accretion rates. A second alternative computation was used in estimating N and P exchanges between the Patuxent estuary and Chesapeake Bay. This is one of the most difficult processes to estimate in estuaries because of the dynamic nature of these systems. In this case, the primary computation was based on box-model estimates of net exchange of N and P (Hagy et al., 2000). Additional estimates of net exchange were made using a water quality model developed for the Patuxent River (Cerco and Cole, 1992) and by subtracting all internal N and P losses from all N and P inputs. All three estimates tended to converge, again not proving the exchange estimate correct, but strongly suggesting that a big error was not made.

17.2.7 Budgets with Apples and Oranges—the Problem of Different Units

Because estuaries (and other ecosystems) are made up of so many different types of living and nonliving components, each of which is studied in detail by specialized sciences and each of these has its own jargon and ways of expressing measurements it is not surprising that ecologists trying to make ecosystem budgets confront a bewildering diversity of units. To take a relatively simple example, consider the ways in which water leaving a watershed might be reported in the literature. A US government hydrologist might express the water flow in cubic feet per second (cfs); water supply professionals work in millions of gallons per day (mgd); hydrologists prefer metric and use cubic meters per second (m^3/s); if there is agriculture in the watershed, the flow might be reported in acre-feet. Of course, countries that only use the metric system will not have this particular problem, but still nutrient concentrations may be expressed in milligram per liter, microgram atoms per liter, or micromolar. While converting from one unit to another is not a difficult computational challenge, the mix makes it difficult to form an intuitive impression of the relative magnitude of different fluxes or to

make quick back of the envelope calculations. Fortunately, there are now numerous on-line Web sites that provide easy conversions, but a print copy of a good set of conversion tables is still a useful part of any coastal ecologist's tool box and it is worthwhile to commit some of the most commonly used to memory. And no matter how simple the arithmetic, every calculation is an opportunity for error and many an embarrassing mistake has slipped into budgets!

17.3 CASE STUDIES

In this section, several case studies of budget applications are presented. These are presented at levels of detail sufficient to make clear why a budget approach was adopted, what questions were being addressed, what understanding was achieved, how data were used or manipulated to conform with requirements of a budget format, and what was missing or uncertain in these budget analyses. Several levels of biological organization were included in these case study examples to make clear the range of potential applications. Several budgets are organized at the "whole ecosystem" level of organization (e.g., entire estuary), while others are at the community (e.g., sea grass bed) or individual (e.g., a fish species) levels of organization. The point is that budgets can be constructed at a variety of spatial and temporal scales (see Book Supplement at www.wiley.com/go/day/estuarineecology for graphic examples and a listing of many budget applications).

17.3.1 Case Study I: Salt and Water Mass Balances: An Approach for Quantifying Estuarine Nutrient Transport, Transformation, and Net Ecosystem Production

An important question in coastal ecology is how estuarine productivity is related to key plant nutrients and dominant physical processes. Commonly, quantitative models are built to explore and evaluate the relationships between biological and physical processes. In their simplest form, such models may be regressions between forcing variables (e.g., river flow, temperature) and an ecological process (e.g., primary production, sediment-water NH_4^+ flux). On the other extreme, spatially explicit hydrodynamic models can be coupled to process-driven biogeochemical models to make high-spatial-resolution predictions of daily, seasonal, and interannual estuarine dynamics. Between simple regression models and complex, spatially explicit deterministic models

is a class of intermediate complexity models, called *box-models*, that quantify biological and physical coupling without the complexity and high cost of modern hydrodynamic biogeochemical models (Pritchard, 1969; Officer, 1980). These ''box-models'' allow estimates of both physical transport and net biogeochemical production of nutrients, O_2, and carbon in estuarine ecosystems from commonly available estuarine data, including nutrient and oxygen concentrations, streamflow, precipitation, salinity, and bathymetry. These mass balance budgets allow us to infer rate processes from commonly available measurements of concentration.

Specifically, box-models are used to compute advective and diffusive transports of salt, nutrients, and other variables in estuarine ecosystems where salinity and freshwater inputs are known. To construct a box-model, an aquatic system must first be divided into defined control volumes or ''boxes,'' where in the simplest case, the entire estuary of interest would be a single box (Fig. 17.2). Boundaries separating adjacent boxes can be defined based on data availability, degree of density stratification, and distribution of salt and water volume among boxes. Coefficients of advective exchange of water and diffusive exchange of dissolved materials between boxes are derived from mass balances of salt and water for each box (Fig. 17.2; Equations 1 and 2). These coefficients are then multiplied by available nutrient concentrations to compute physical transport and
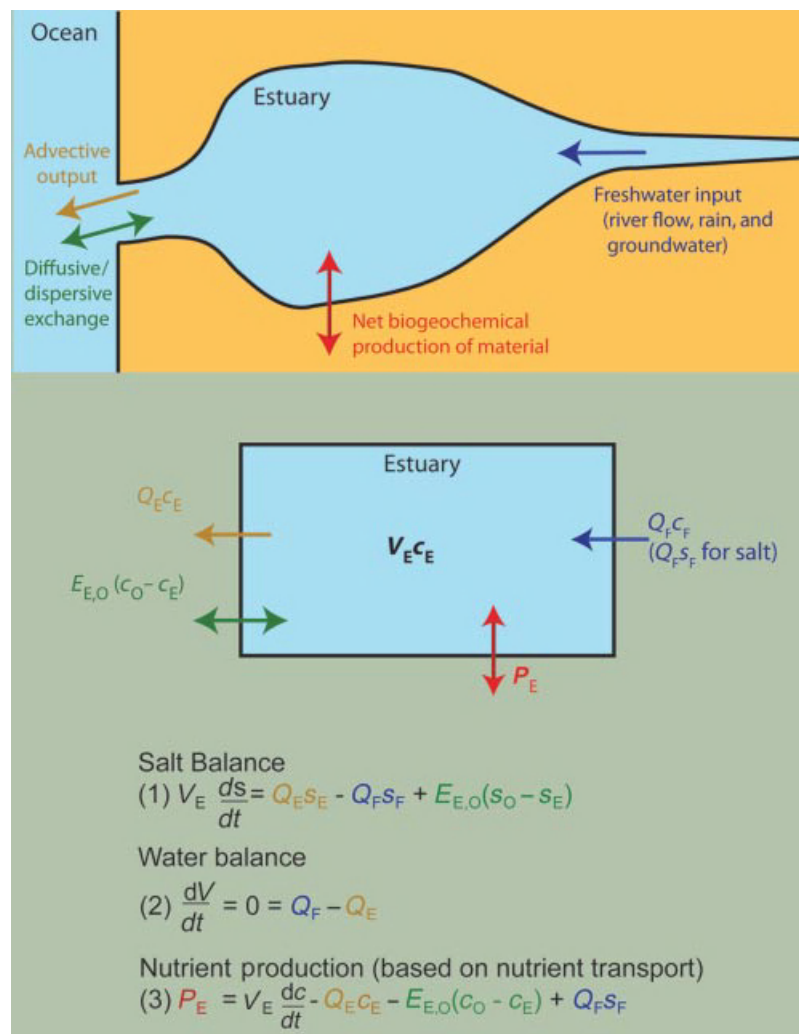
FIGURE 17.2 Schematic diagram of simple box-model computation for an estuary receiving freshwater from a single river and connected to the ocean by a single channel. Salt, water, and nutrient balances are represented by equations 1–3, respectively. Q_F = freshwater input volume, Q_E = water output from estuary, $E_{E,O}$ is diffusive/dispersive exchange between estuary and ocean, V_E = the volume of the estuary, and P_E = the net production rate of nutrient, O_2, or carbon in the estuary. s_O = ocean salinity, s_F = freshwater salinity = 0, and s_E = estuary salinity. c_O = ocean nutrient/O_2/carbon concentration, c_F = freshwater nutrient/O_2/carbon concentration, and c_E = estuary nutrient/O_2/carbon concentration.

exchange of nutrients between boxes, or between the estuarine box and the adjacent ocean (Fig. 17.2). In the next step, any residual nutrient remaining from a mass balance of the physical transports of nutrients into and out of each box represents net biogeochemical production of that nutrient, which can serve as a proxy for biological activity (Fig. 17.2; Eq. 17.3). In the specific cases of net biogeochemical production of O_2, dissolved inorganic carbon, or dissolved inorganic phosphorus, net production rates can be used to quantify net ecosystem production (see Book Supplement at www.wiley.com/go/day/estuarineecology for examples and other applications of this approach).

Box-models are useful tools for scientists and managers alike. Construction of the model is based entirely on previously collected data, so expensive and time-consuming field and laboratory efforts are avoided. The equations used to build the models are simple and avoid the need for extensive computing power. Box-models yield rates of carbon and nutrient production and consumption, which cannot replace rigorous rate measurements but can provide rate estimates to guide future work and constrain extrapolation of experimental rates.

Lastly, the box-model methodology is straightforward and flexible and can therefore be applied to a diverse array of estuarine systems, as has been done within the LOICZ (http://nest.su.se/mnode/) program (Gordon et al., 1996). The approach is limited, however, in that only *net* rates can be computed, so that the many specific processes contributing to these net rates cannot be quantified separately. In systems with limited hydrologic and water quality monitoring, the spatial and temporal scales of model computations may also be limited. Lastly, a common assumption that boxes are completely mixed with uniformly distributed constituent concentrations may be erroneous in some cases.

The Patuxent River estuary (Maryland, USA) is one of many systems where a box-model was used to investigate nutrient cycling (Hagy et al., 2000; Testa and Kemp, 2008) and examples of seasonal cycles of box-model-computed rates of net O_2, dissolved inorganic nitrogen (DIN), and dissolved silicate (DSi) production in both surface and bottom layers of the estuary were developed (Fig. 17.3). The rates illustrate the connection of net O_2 production (i.e., net ecosystem photosynthesis) in the surface layer during spring to the net uptake of DIN and DSi, which are used to fuel plant production. In the bottom layer, summer peaks in net O_2 consumption co-occur with seasonal
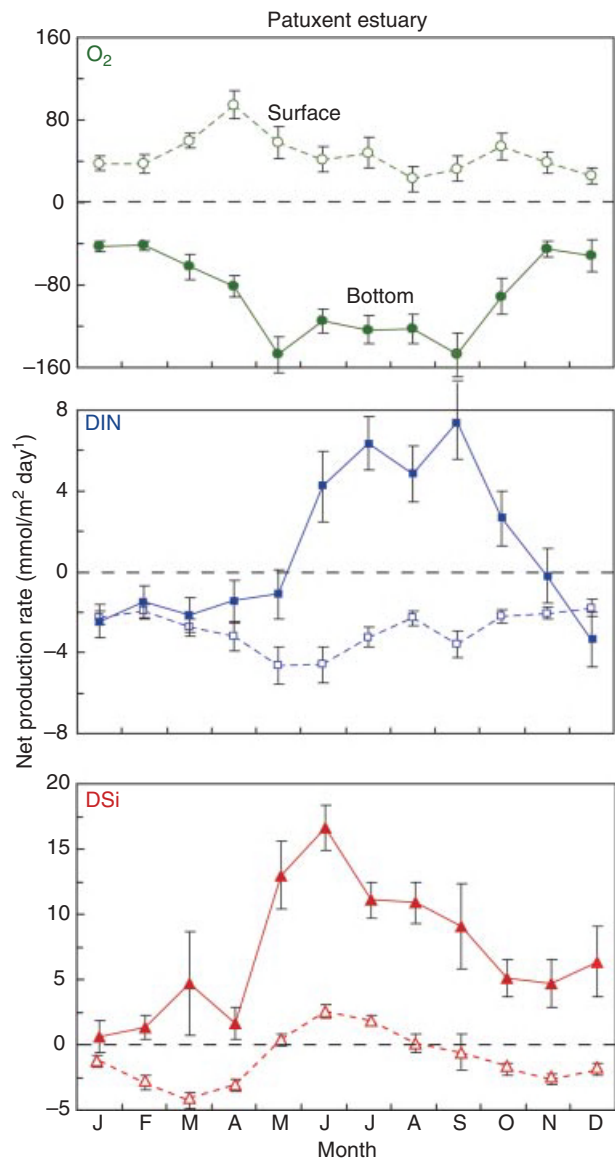
FIGURE 17.3 Monthly mean rates of net biogeochemical production of surface and bottom-layer (top) O_2 (surface rate corrected for air–water exchange), (middle) DIN, and (bottom) DSi computed by the box-model for the surface and bottom layers in the Patuxent River estuary. Monthly means ($\pm$ standard error) were calculated for the years 1985–2003. Horizontal dashed lines are drawn at net production rates equal to zero. *Source:* Data and figure are from Testa and Kemp (2008).

peaks in net production of DIN and DSi, illustrating the aerobic respiration of organic matter and coupled remineralization of nutrients. Box-modeling has been used extensively in other systems to answer a range of scientific questions (see Book Supplement at www.wiley.com/go/day/estuarineecology for additional examples).

17.3.2 Case Study II: Organism-Scale Nitrogen Budget: Mussels in a Salt Marsh Ecosystem

Salt marshes are important and obvious features of many temperate zone ecosystems (Chapter 6). Coastal marshes occur from tidal freshwater portions of estuaries to high salinity areas often associated with coastal lagoons. In most cases, these systems are characterized by high rates of autotrophic production and high to very high standing stocks of plant biomass and substantial animal populations. Tidal marshes provide essential habitat for many plant and animal populations and provide a complex buffer between the uplands and open waters of estuarine and coastal ecosystems. There have been many studies of tidal marshes during the past 50 years and some have used a budget framework for analysis and synthesis (Teal, 1962; Nixon and Oviatt, 1973).

In this case study, we chose to summarize work conducted in a Southern New England salt marsh for several reasons. First, a nitrogen budget of an important marsh species (the ribbed mussel, *Geukensia demissa*) was developed and is a major focus in this case study. Second, the results of that budget were placed in the context of a nitrogen budget for the full salt marsh ecosystem and hence we can see the power of a nested or hierarchical set of budgets. Finally, these investigators applied several of the techniques listed earlier to more accurately scale-up rate processes made at small spatial and temporal scales to the spatial scale of the full marsh system for seasonal and annual time periods (Jordan and Valiela, 1982). The basic question investigated in this study concerned the role of a filter-feeding bivalve in the nitrogen budget of a salt marsh ecosystem.

The study site was the Great Sippewissett Marsh located on Cape Cod, MA. The marsh has one exchange channel with adjacent coastal waters (Buzzards Bay), and the marsh is flooded twice daily by substantial tidal flows (~1.6 m tides). The major habitats of this marsh include sandy creek bottoms bare of vegetation, salt pans with limited vegetation, mats of blue-green algae and purple sulfur bacteria on mud flats, dominant low marsh vegetation characterized by short *Spartina alterniflora* and a small amount of tall *S. alterniflora* along creek banks, high marsh areas vegetated with *Spartina patens* and *Distichlis spicata*, and an abundant ribbed mussel population ($34–734$ individual m^{-2}) representing about 75% of the filter-feeding bivalves in the marsh system.

The nitrogen budget of the ribbed mussel and the budget for the full salt marsh system are summarized in Figure 17.4. In the ribbed mussel budget, the mussels connect with the marsh system via filtration of particulate nitrogen (PN) delivered to the marsh from tidal waters. Major losses include biodeposition of nonassimilated nitrogen particles to the marsh surface, net growth of mussels, excretion of ammonium, release of gametes, and production of byssal threads connecting mussels to hard substrates. There were no measureable losses of nitrogen as dissolved organic nitrogen (DON), mortality, or recruitment. The salt
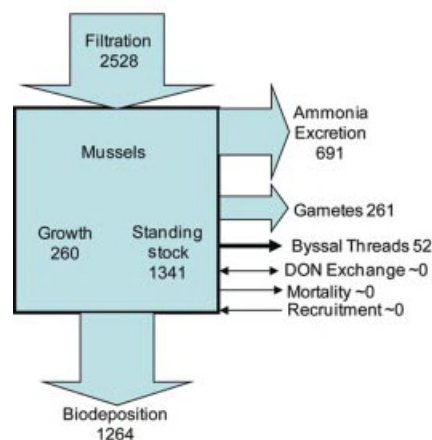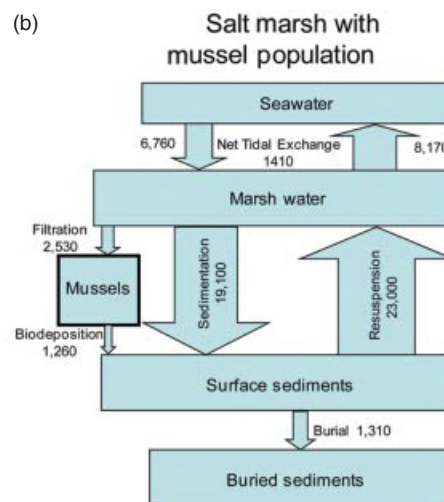
FIGURE 17.4 Two nitrogen budgets developed for a New England, United States, salt marsh ecosystem. (A) An annual-scale budget for the mussel population for Great Sippewissett Marsh and (b) an annual-scale budget for the full marsh ecosystem with the mussel population highlighted. Nitrogen flows for both budgets have units of kg N/year, except for mussel standing stock, which has units of kg N. *Source:* These budget diagrams were adapted from Jordan and Valiela (1982).

marsh budget for PN is more complex and involves exchanges of PN associated with tidal exchanges with marsh water. Sedimentation and resuspension of PN in the marsh appear to be dominant processes. Filtration and biodeposition of PN by mussels is also shown on the left side of the diagram as is long-term burial of PN to deeper marsh sediments. While mussel filtration and burial of PN are smaller processes (3840 kg N/year), they are about the same as the net of the much larger processes of PN sedimentation and resuspension (3900 kg N/year).

The details concerning measurement techniques used to evaluate the ribbed mussel nitrogen budget are beyond the scope of this case study, but several features deserve mention because they play so strongly into budget development. First, mussel abundance was a keystone variable used in estimating many of the rates used in the budget. If mussel estimates were not right, then the budget would be inaccurate in many respects. Mussels were intensively sampled along creek banks, where densities were very high, and from two marsh zones (densities lower and different between zones). These detailed measurements were scaled up to the system level using area estimates of creek and marsh types, basically following methods suggested by Schneider (1994) and described earlier in this chapter. Second, these investigators used field-based methods for estimating rates whenever possible because such measurements tend to preserve realism and, if done carefully, do not sacrifice too much experimental control.

17.3.3 Case Study III: Chesapeake Bay Organic Carbon Budget

Estuaries such as Chesapeake Bay are among the most productive systems in the biosphere. Some aspects of this high level of production are due to large nutrient inputs from a variety of sources and to the diversity of primary producers typically found in these systems, including phytoplankton, benthic micro- and macroalgae, submerged aquatic macrophytes (sea grasses), and tidal marshes. In addition, organic carbon enters these systems from rivers and sometimes from the coastal ocean. Once in the estuary, this organic carbon has a variety of fates depending on origin (terrestrial vs *in situ* production), form (particulate vs dissolved), and degree of lability (susceptibility to decomposition or use in food webs). A number of questions arise from these simple observations, including are estuaries efficient traps for organic carbon resulting in organic enrichment of estuarine sediments; is physical transport of organic carbon (inputs from the land and burial) larger or smaller than biological production and losses; how

does organic carbon availability influence or regulate estuarine fisheries yields; what is the balance between production (P) and respiration (R) in these systems; and what are the implications of systems wherein P>R (net autotrophic) or P<R (net heterotrophic).

To examine these questions, Kemp et al. (1997) developed a mass balance of organic carbon fluxes for the main stem portion of Chesapeake Bay. The goal was to quantify the major external inputs, internal production, sinks, and transport of total organic carbon (TOC) in this large estuarine system. Comparisons were also developed between the relative importance of biological versus physical sources and sinks of organic carbon and the balance between system gross production and respiration (Net Ecosystem Metabolism, NEM; see Chapter 15).

Chesapeake Bay is among the largest estuarine systems in the USA and is characterized by high rates of both primary production and fisheries harvest. Key bay features include relatively shallow water depth that promotes efficient nutrient cycling between the water column and benthos and relatively long water residence time that favors retention and recycling of materials rather than export. Both features promote high rates of organic carbon production. The main stem Bay is characterized by three distinct salinity zones where major processes differ. The upper Bay is shallow, very turbid, has relatively low rates of *in situ* algal production, and is heavily influenced by flow from the Susquehanna, the major river entering the Bay. The mid-Bay is clearer, deeper, experiences chronic summer hypoxia and anoxia, and has much higher rates of algal production. Finally, the lower Bay is of intermediate depth, clearer than the mid-Bay, less hypoxic, and has algal production rates intermediate between the other zones. Kemp et al. (1997) used these zones in developing the mass balance because differences among zones were clear and data were available to treat each zone as a separate unit.

The organic carbon budget for this estuary is shown in Figure 17.5. While apparently quite simple (there are only five inputs and five loss terms), evaluation of these terms required a substantial amount of information that was available from a variety of sources. For example, algal production measurements were made at many locations and seasons using oxygen- and ^{14}C-based techniques. Both plankton and benthic respiration rates were made using oxygen-based measurements, and sulfate reduction measurements were used to assess anaerobic respiration in sediments. Submerged macrophyte and tidal marsh production was estimated using aerial images of plant distribution coupled with literature rates of production per unit area. Inputs of organic carbon

Production (P)

Algae
3622

Vasc. Plants
281

Inputs (I)

Susq. R
151

Tributaries
110

Atmosphere
24

285

TOC
Pool

Outputs (E)

Ocean export
281

Burial
217

Fisheries
45

543

Net ecosstem metabolism

$P - R = 270 \times 10^9$ g C/year

or

$I - E = 258 \times 10^9$ g C/year

Plankton
2503

Benthos
899

Respiration (R)

TOC fluxes
10^9 g C/year
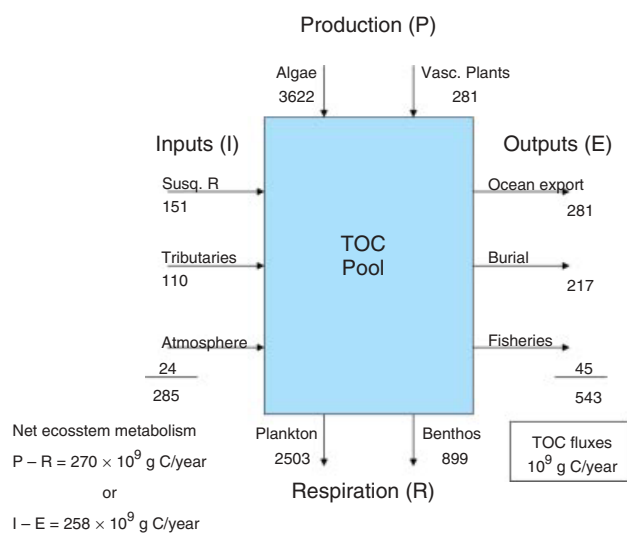
FIGURE 17.5 Estimated mean average values for major TOC fluxes in the mainstem Chesapeake Bay. Fluxes are grouped as Inputs (I), Outputs (E), Production (P), and Respiration (R). Net Ecosystem Metabolism (NEM) for the mainstem Bay is also provided. *Source:* Diagram was adapted from Kemp et al. (1997).

from the Susquehanna River were based on measurements of water flow coupled to measurements of TOC concentrations. Fluxes of TOC from the tributaries to the Bay and fluxes from the Bay to the coastal ocean were based on results of water quality model simulations for an average water year. Estimates of long-term burial of organic carbon in the accreting sediment column were based on ^{210}Pb estimates of sediment deposition coupled to POC concentrations in the sediment column. Finally, TOC losses due to fisheries yields were based on catch records and converted to carbon units.

Results from this mass balance indicate a good understanding of the system. Organic carbon outputs (both biological and physical) accounted for about 94% of all inputs indicating a nearly balanced budget and strongly suggest that major input and output terms have been adequately captured. In river-dominated tidal systems such as Chesapeake Bay, it is easy to assume that physical processes such as river inputs of organic carbon from the very large watershed and tidal transport of organic carbon to the coastal ocean would dominate the budget processes. However, the opposite appears to be the case. Biological production and consumption of organic carbon represented 93% of TOC inputs and 87% of all losses. Thus, internal biological processes dominated the overall budget rather than physical processes of transport and river inputs. Much of the enhanced

production in this eutrophic estuary is based on nutrient inputs from the adjacent watershed. There was also a distinct gradient along the axis of the estuary regarding the balance of production and respiration of organic carbon. In the upper Bay, in the zone strongly influenced by inflows from the Susquehanna River, R exceeded P and the system was net heterotrophic (meaning that more organic carbon was respired than produced *in situ*, indicating the importance of river-borne organic carbon as an additional source). Other regions of the Bay, with less river influence, were net autotrophic indicating potential for use of organic carbon for fish production and export to the coastal ocean. Overall, the bay was net autotrophic. Finally, fisheries yields represented a small fraction (~1%) of the TOC input to this system but a more substantial fraction of the NEM (~17%).

For the past 25 years, there has been intense interest in restoring this eutrophic estuary to a more pristine condition where hypoxia and anoxia are sharply reduced, algal blooms diminished, and sea grass communities restored. Budgets provide managers with quantified estimates of the relative importance of organic carbon sources and sinks and that understanding can aid management decisions. In the case of Chesapeake Bay, managers must balance the need for a productive ecosystem to support fisheries production with the desire to reduce detrimental effects of anoxia and habitat loss resulting from excessive production in this currently overfertilized estuary.

17.3.4 Case Study IV: An Upside-Down Budget: Pre-European and Contemporary Nutrient Inputs to Narragansett Bay, RI

As we have discussed earlier, budgets are very useful in providing a disciplined, quantitative framework for formulating a conceptual model of the system of interest and showing the relative importance of different sources, sinks, and transformations within the system. However, they can also be helpful for documenting and illustrating the magnitude of human impact in estuaries and other coastal ecosystems. One of the most dramatic ways in which ecologists use them for this purpose is by constructing historical or even prehistoric budgets and by comparing them with contemporary mass or energy balances. Good examples include Elmgren's (1989) comparison of biological energy flow in the Baltic Sea in the early and late twentieth century, the Kemp et al. (2005) assessment of eutrophication history of Chesapeake Bay, and a recent comparison of nutrient budgets for several European coastal areas before, during, and after

periods of cultural eutrophication (Artioli et al., 2008). Here, we illustrate a more extreme example comparing the nitrogen (N) and phosphorus (P) inputs to Narragansett Bay just before extensive European contact with recent conditions (Nixon, 1997).

Narragansett Bay is a relatively small (234 km², 8.6 m mean depth) urbanized estuary in southern New England just south of Cape Cod. Its written history began with a visit from the explorer Giovanni da Verrazzano in April of 1524. While Verrazzano later recorded many details about the Narragansett Indians he encountered and gave some useful description of the geography of the area, he failed to make a single measurement of N or P entering the bay from any source! Not surprising, of course, since P was not discovered until 1669 and N until about 1770 and our recognition of the importance of these elements in plant productivity would not come until the latter 1800s. We would not be able to measure them in the low concentrations found in rivers and seawater until the late 1800s and early decades of the twentieth century. With no measurements, how can we make even rough N and P budgets for that prehistoric time?

The simple answer is that a good ecologist always keeps an envelope handy for doing those back of the envelope calculations talked about earlier. And we make lots of assumptions (a nice word for informed and explicitly stated guesses). Some parts are easy. While the direct discharges of sewage treatment plants now provide a lot of N and P to the bay, they did not exist before the late 1800s (Nixon et al., 2008). In fact, the human population density was low enough (probably about 2–4 people km²; Nixon, 2004, compared with 320–390 km² in Massachusetts and Rhode Island today) that it seems safe to ignore human waste as a significant source of N or P to the prehistoric bay. Similarly, while atmospheric deposition today is a significant source of reactive N to the watershed and the bay itself, that reactive N gets into the atmosphere from the combustion of fossil fuels—not a significant source before the industrial revolution. Even today, atmospheric deposition of P is very small in this area and can certainly be neglected during Verazzano's visit. The rivers entering the bay today carry high concentrations of N and P and have been doing so since the late 1800s/early 1900s (Nixon et al., 2008), but the watershed today is very different from the landscape of the 1500s. In addition to sewage treatment plants that discharge to the rivers, hundreds of thousands of people in the watershed discharge their wastes into septic systems that leach N (and maybe some P) into groundwater that flows to the rivers; large areas are paved with impervious surfaces that carry N and P through storm drains to the rivers; there is some agriculture that uses synthetic fertilizers that may wash off and reach the rivers. There is no compelling evidence that the precontact Narragansett Indians practiced significant agriculture (Nixon, 2004)—but even if they did, synthetic fertilizer was hundreds of years in the future (and a possible fish added to a hill of corn would not have been a significant source of N to the bay). The evidence we have from modern analyses of streams and rivers draining minimally disturbed forests such as those surrounding Narragansett Bay in the 1500s suggest that reactive N and P concentrations would have been very low, as they still were in unpolluted rivers and streams draining into the bay in the late 1800s when the first measurements became possible (Nixon et al., 2008). Using those concentrations and assuming that the mean annual river flow to the bay has not changed, we can calculate the fluxes of N and P to the bay from land under prehistoric conditions. Of course, then as now, the bay was connected by tidal flows and estuarine circulation with the offshore waters of Rhode Island Sound and we might assume that that exchange has remained largely unchanged (and, admittedly, quite uncertain). With these assumptions, we can put together rough prehistoric N and P budgets to compare with those derived from contemporary measurements (Nixon et al., 1995, 2008; Fig. 17.6).
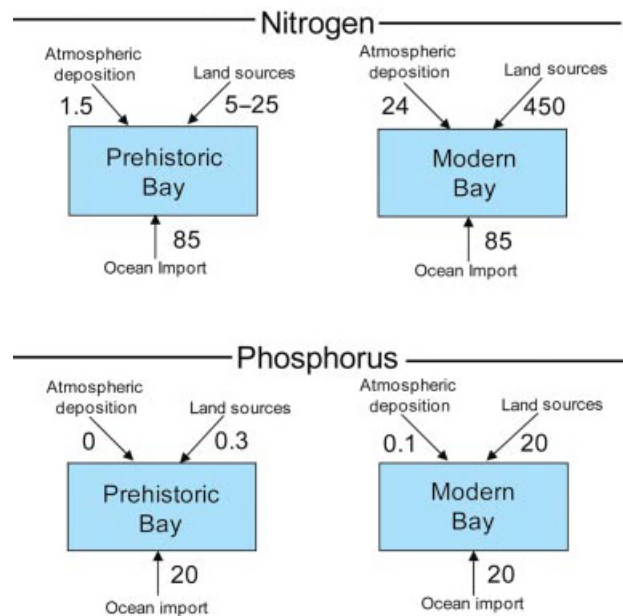
FIGURE 17.6 Comparison of estimated annual inputs of dissolved inorganic N and P to Narragansett Bay, RI/MA during prehistoric and modern times. *Source*: modified from Nixon, 1997. Units are 10^6 moles/year.

Two dramatic differences stand out: first, the much larger amounts of N and P that are now being delivered to the bay—N has increased by a factor of 5 or 6 and P has doubled. Second, the major source of N has switched from the coastal ocean to land and land has become equal to the sea as a source of P. In other words, the budgets are now upside down compared to the prehistoric situation. Because this flip has become so common in the developed world with large urban areas and intensive fertilizer and animal husbandry, it seems surprising to think that in earlier times the major source of estuarine productivity may have been nutrients from offshore waters brought into the systems through estuarine circulation. These nutrients may have been captured and concentrated by macroalgae (e.g., kelp beds), sea grass meadows, and epibenthic microalgae as well as dense beds of filter-feeding animals such as oysters and mussels. Certainly, the anecdotal reports of early Europeans as well as abundant shellfish middens from coastal Indian populations suggest that the estuaries downstream from what must have been nutrient-tight forest and mature grassland ecosystems were highly productive. The only sources of N and P to those upstream watersheds were biological fixation, lightening, and rock weathering—it seems unlikely that enrichment from land drainage was the major support for robust coastal food chains.

17.4 MASS BALANCE APPLICATIONS FOR SCIENCE AND MANAGEMENT

We conclude this chapter by presenting examples of mass balance approaches used to advance scientific understanding of estuarine function and assist in evaluating estuarine management options and actions. So, these examples represent for modern ecologists Archimedes firm spot to stand and move forward, if not the earth, at least our understanding of estuarine system function.

Included in these examples is an effort using mass balances to explore factors regulating the amount of nitrogen exported from multiple estuaries to the coastal ocean. Mass balances were used to see if a general pattern governing nutrient export could be found. The second example involves use of a mass balance to examine the effects of a "hot spot" for nutrient losses along an estuarine gradient. The final example involves use of mass balances to guide development of a nutrient strategy for a large estuarine system. In this case, a series of budgets were

developed. An early budget reached very different conclusions having important management implications than budgets developed a short time later. This example demonstrates the progressive improvements possible using a budget framework in developing management plans.

17.4.1 Budgets as Building Blocks: Nitrogen Export from Estuaries

All the budgets presented so far have used mass balances as a synthesis framework for examining a single "system", regardless of that system being an individual, a population, a community, or an ecosystem. However, budgets, or parts of budgets, can also be used in cross-system comparisons to give a broader perspective. Sometimes, this is helpful simply to give us a sense of scale. For example, is the marsh for which we have so painstakingly developed a detailed sediment budget likely to be representative of other marshes in the region, or is it really a tiny piece of the landscape that may not be a good platform for making broad conclusions about marshes in general? By comparing many budgets, we can also gain new insights about processes that may influence system behavior and help shape the individual budgets themselves.

An example from our own experience emerged at a week-long workshop held on an isolated island off the southern New England coast. Ecologists with experience in a wide range of estuaries and bays were gathered to discuss the scientific evidence about what processes governed the fate of nitrogen (N) and phosphorus (P) as these nutrients passed from watersheds on land to the continental shelf (Galloway et al., 1996). As we compared the budgets developed for the systems we each studied, it became clear that the fraction of N entering each estuary that actually passed through to the coastal ocean varied widely (Table 17.1).

"Trapped" together for many days in our comfortable hotel, we had many opportunities to speculate about the causes for such dramatic differences. And the group contained a diverse mix of experts in estuarine physics, biogeochemistry, geology, biology, and ecology. Finally, the group had a collective "aha!" moment as we plotted the fraction of N that passed through each system against the mean annual water residence time of the system (Fig. 17.7). In hindsight, it seems intuitive that the longer an atom of N spends in an estuary the greater is the likelihood that it might be removed and lost to the atmosphere as N_2 gas through denitrification (the respiration of organic matter using nitrate rather than oxygen, Chapter 3) or anammox (the formation of organic matter from CO_2 by specialized bacteria that produce N_2 gas from

TABLE 17.1 A summary of total nitrogen fluxes reported for annual-scale budgets for a selection of 11 different estuarine systems

Estuarine/ Coastal System	Inputs					Net Accumulation		Outputs		
	Direct Atmospheric Deposition	Nitrogen Fixation	River Inputs	Point Sources	Total	Water Column	Bottom Sediment	Denitrification	Fisheries	Export Ocean
Baltic Sea	68	26	109	14	217	16	11	165	5	20
Guadalupe Estuary, dry year	40	48	345	115	548	25	1	320	35	167
Chesapeake Bay	113	?	565	260	938	~0	327	245	84	282
Patuxent Estuary	73	?	816	193	1082	0	386	403	27	141
Narragansett Bay	90	~0	1200	570	1860	~0	238	390	13	1090
Delaware Bay	100	?	1800	Combined w/river inputs	1900	~0	255	925	Small	720
Guadalupe Estuary, wet year	40	48	1900	70	2058	30	65	320	85	1558
Potomac Estuary	113	?	1277	705	2095	0	837	330	10	918
Ochlockonee Bay	82	<3.5	5910	0	5996	0	115	640	Very small	5240
Boston Harbor	200	0	735	8160	9095	0	335	910	Very small	7850
Scheldt Estuary	?	?	10050	3350	13400	?	1030	5420	?	6950

Data were available for the Guadalupe estuary for both dry and wet years. Data for all systems but the Patuxent were reported in Nixon et al. (1996); Patuxent estuary data were from Boynton et al. 2008. Details concerning data sources and computations can be found in these papers. Systems are arranged from lowest to highest areal loading rate (column 6). All entries in the table have units of millimoles N/m²/year.
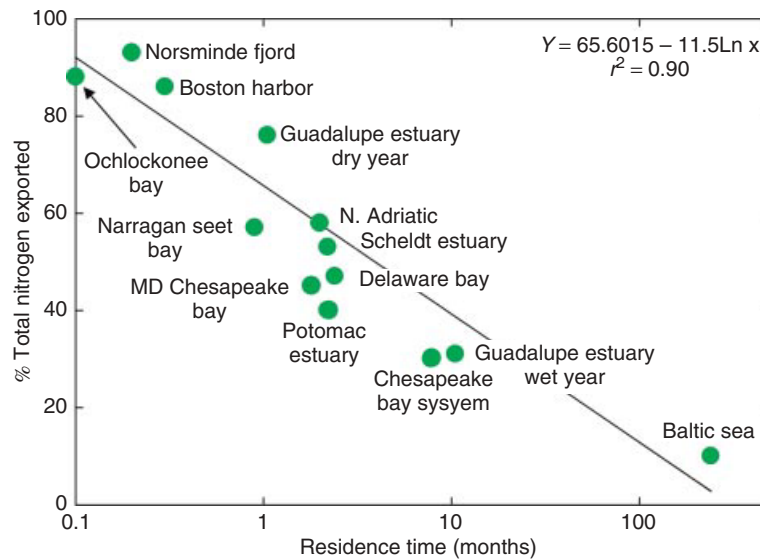
FIGURE 17.7 The fraction of total N input from land and atmosphere that is exported to near-shore shelf waters from a sample of estuaries and other coastal systems as a function of mean annual water residence time. Mean water residence time was calculated by the freshwater fraction method (mean fresh water contained in the estuary calculated from salinity divided by the inflow of fresh water; see Sheldon and Alber, 2006). *Source:* Figure was adapted from Nixon et al. (1996).

nitrite and ammonium) or that it might be buried and accumulate in sediments. But the N cycle is so complex and influenced by so many factors that it was not obvious that a clear pattern might emerge with a single variable.

There are many other examples of insights gained from cross-system comparisons of results from budget type studies, including the export of N from watersheds (Howarth et al., 1996), the rich literature on allometric scaling relationships for individual organisms and populations (Harris et al., 2006), benthic-pelagic coupling with water depth (Kemp et al., 2001), and a wide range of other ecosystem processes (Cole et al., 1991).

17.4.2 An Estuarine "Hotspot" for Nutrient Losses

The Patuxent River, a tributary of Chesapeake Bay, is a partially mixed coastal plain estuary. The Patuxent River watershed encompasses 2256 km² of land, 143 km² of tidal waters, and 29 km² of tidal marshes. The river and estuary are about 170 km in total length; the lower 95 km are tidal. The upper portion of the tidal estuary is narrow (50–300 m wide), very turbid ($K_d = 3.0 \text{ m}^{-1}$), vertically well mixed, and has a tidal range of 0.5–1.0 m and an average depth of 1.1 m. Importantly, this portion of the estuary (yellow area in Fig. 17.8) is flanked by extensive tidal freshwater and salt marshes with the ratio of marsh area to river distance ranging from 0.4 to 0.8 km²/ km of river.

The Patuxent is among the most well-known and studied Chesapeake Bay tributaries because of a long history of management debate, court cases, and eventual management actions aimed at water quality and habitat restoration. The Patuxent watershed was quite rural before world war II having a population basically unchanged since the census of 1790. However, during the late 1950s and early 1960s, the upper basin developed rapidly with agricultural and forested lands converted to suburban and urban uses. Sewage treatment plants began discharging into the river in 1963 and now discharge about 70 million gallons per day, a volume that is slightly larger than river flow during low flow periods. Nutrient load increases have been documented since 1960 and monitoring and research programs have reported increases in algal production and biomass, loss of sea grass communities, expansion and intensification of seasonal hypoxia, and severe impacts on benthic animal communities. Commercial fishing activities in this estuary have been severely reduced since the mid-1980s.

In response to Federal court actions, a nutrient reduction plan, focused on point sources, was developed. Beginning in the mid-1980s, a phosphate detergent ban and phosphorus removal at all major sewage treatment plants was instituted, and by 1993, nitrogen was also being removed via denitrification during warm periods of the year at all major treatment plants. However, diffuse nutrient source reductions were not part of this plan. Using the

multidecade Patuxent water quality data set, Testa et al. 2008 were able to show that nutrient concentrations declined throughout the estuary and algal production, biomass, and respiration also declined in the upper, but not the lower, estuary. The estuary remains "listed" by EPA as impacted for several water quality variables. Because of persistent water quality issues, a TMDL (total maximum daily load) analysis was required for this estuary and a preliminary modeling system was developed. One result of this effort was that a coupled hydrodynamic water quality model consistently overestimated concentrations of DIN through the portion of the estuary where tidal marshes were prevalent; the water quality model did not have a tidal marsh component. When this discrepancy became clear, Williams et al. (2006) initiated additional water quality analyses of this problem and found a very strong correlation between tidal marsh area and the difference between measured and simulated nitrate concentrations.

Resources and data were not available to develop a marsh component to the water quality model, but efforts were made to develop a nutrient mass balance for the estuary with particular emphasis on the section of the estuary having tidal marshes. A key question revolved around the quantitative capacity of the marshes to serve as a substantial sink for N and P. A multiyear N and P budget was developed (Boynton et al., 2008) for the full estuary, and a summary of the N budget focusing on the tidal marsh-dominated portion of the estuary is provided in Figure 17.8. Data sets needed for this computation included burial rates of N in subtidal areas and intertidal marshes and denitrification rates in these same habitats. A box-model (another type of mass balance model) was developed for estimating physical nutrient transport between the oligohaline (salinity of about 0.3–3) and mesohaline (salinity between about 3 and 16) portions of the estuary (Hagy et al., 2000). Direct measurements of river flow and nutrient concentrations at the head of tide were developed by the USGS (2004) to estimate riverine nutrient inputs, and a landscape model was used to estimate inputs from the sides of the estuary.

In the upper Patuxent, TN input amounts to about 5440 kg N/day and this represents about 80% of the TN input to the entire estuarine system. In the upper estuary, about 46% of inputs were lost via long-term burial and denitrification. Loss processes occurring in adjacent tidal marshes accounted for 64% of all losses in this region of the estuary. While this region represents only 12% of estuarine surface area (and only 3% of the full basin and estuary!) about 45% of all internal losses occur in this small zone of the estuary. This zone of the estuary removes about 900,000 kg N/year,
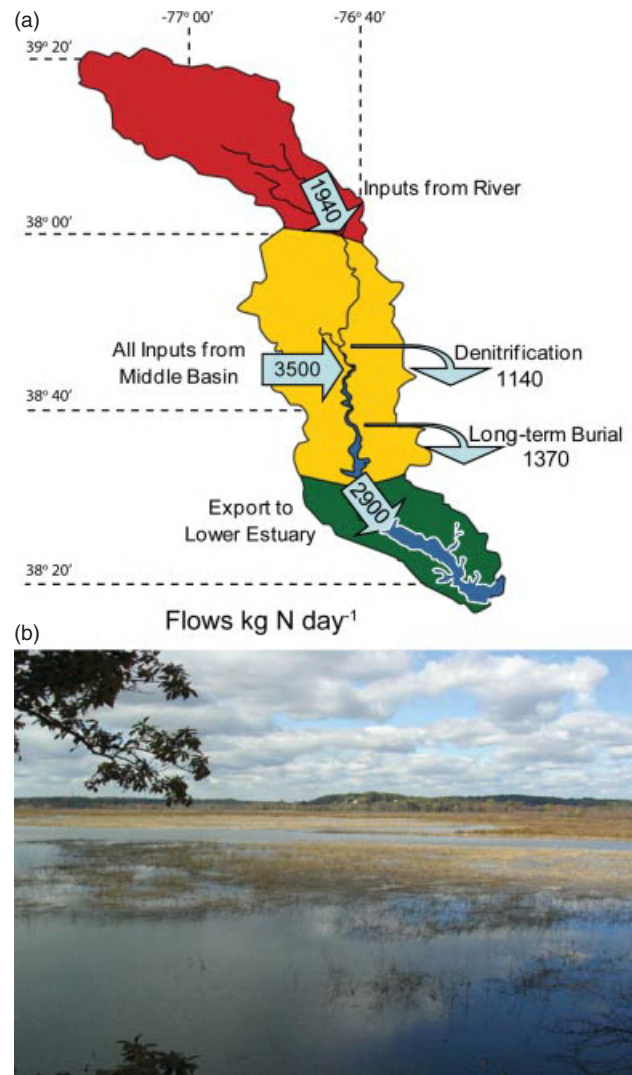
FIGURE 17.8 A map of the Patuxent River basin and estuary (a) with summary nitrogen budget results for the middle basin (tan color) and the portion of the estuary associated with the middle basin and (b) a photograph of the tidal marsh at high tide typical of this section of the estuary. *Source:* Data were adapted from Boynton et al. 2008.

equivalent to the N removed via denitrification at all nine of the large sewage treatment plants in this basin. Clearly, this estuary does not simply convey nitrogen from its drainage basin to the mesohaline estuary and to Chesapeake Bay. Thus, this budget analysis illustrated the quantitatively important role of tidal marshes as a nutrient loss hot spot in the landscape. Accreting marshes, such as those in the Patuxent, act as an efficient "ecosystem-scale kidney" and should continue to be protected for the ecosystem services that they provide. However, should the tidal marshes of the Patuxent fail to keep pace with rising sea level, as has occurred in about 50% of other Chesapeake

Bay tidal marshes, the nutrient removal associated with marshes would be lost; further still, eroding marshes could serve as a source of organic matter and nutrients, reversing the current beneficial role of marshes.

17.4.3 Muddles, Mud, and Management

In earlier sections, we suggested that even rough budgets done on the ''back of an envelope'' could be useful and noted that budgets can often help us avoid big mistakes. It follows that these properties might make budgets useful tools for managers and policy makers. Or not, depending on how good the data and assumptions are that go into the budget.

About 30 years ago, the US Environmental Protection Agency (EPA) undertook a major study of nutrient inputs to Chesapeake Bay. The work was motivated in large part by concerns that nutrient inputs had been increasing and stimulating blooms of phytoplankton and epiphytes growing on sea grass leaves that were shading out the submersed grass beds (e.g., Bayley et al., 1978). It took a lot of work to obtain measurements of all the forms of nitrogen (N) and phosphorus (P) coming into such a large estuary from atmospheric deposition, rivers, agricultural runoff, and sewage treatment plants, and the EPA and academic scientists summarized the results in a major report (Smullen et al., 1982). With estimates of the total annual inputs from atmosphere and watershed in hand, the EPA then asked an important and interesting question, a question growing naturally out of the mass balance model—how much of the N and P entering the bay passed through it and out to the continental shelf? They attempted to answer this question by making direct measurements of the concentrations of N and P in the water at the mouth of the bay as it ebbed and flooded while they simultaneously measured and modeled the current speed at various places and depths, so they could multiply the volume of water by the concentrations to calculate the total N and P transported in each direction. It seems an appealing and straightforward approach to answer the question: flux of N or P in at the mouth during flood tide minus the flux out during ebb tide = net exchange. The net exchange could then be compared with the measured total input from land and atmosphere.

The results of all the work at the mouth of the bay seemed to show that there was very little net transport of N or P between the bay and the continental shelf. As Smullen et al. (1982) concluded, ''Nearly all the materials that enter the bay remain there; nutrients trickle out of the Bay mouth at a very slow rate.'' They went on to emphasize the ''profound implications for management ... even

if nutrient loads were drastically reduced, bay-wide improvement of water quality would be very slow.''

Such a depressing conclusion seemed surprising, at least to some of us. While it was well known that Chesapeake Bay, like many other estuaries, trapped virtually all of the sediment that was delivered by rivers (Biggs, 1970; Schubel and Carter, 1977), N and P are much more dynamic. Nutrients are taken up by organisms and rapidly cycled within the ecosystem; they are also actively exchanged between sediments and the water column—why would they behave like inorganic silts and sands and clays? Fortunately, the EPA study had also summarized data on the amount of sediment entering the bay during the same period that the nutrient inputs were being measured. It seemed that a useful back of the envelope calculation might be to estimate the N and P content of the sediments in the bay if all the nutrients and sediments were accumulating together in the system. The result suggested that the sediments should be about 4% N and 0.34% P, values that are considerably higher than those measured in Chesapeake Bay sediments. This suggests that some of the N and P inputs must be exported to the ocean. The message in the mud seemed clear—Chesapeake Bay could not be storing all or even most of the N and P that entered (Nixon, 1987).

The back of the envelope calculation stimulated EPA to support a much more thorough budget analysis of N, P, and sediments in Chesapeake Bay. Important outcomes of that analysis included the identification of shoreline erosion as a much more important source of sediment to the bay than had previously been appreciated, the separation of N removal from the bay through denitrification compared with the burial of N in sediments, and an improved assessment for the role of fisheries landings in removing N and P from the system (Boynton et al., 1995). The end result was that Chesapeake Bay appeared to be storing just a bit more N and P than the back of the envelope calculation suggested, but certainly not all of the nutrients. The implication for management was much more positive—reducing nutrient inputs should have a relatively rapid impact on water quality conditions in the bay.

What went wrong? Actually, nothing—the process of doing science and of managers interacting with scientists evolved as it should. It just took longer and probably cost more money and effort than anyone thought it would at the start. EPA adopted a good conceptual framework with a budget approach. However, they chose to try to measure a very difficult exchange—the net flux at the mouth of the bay. This

flux arises because of small changes in concentration and the integration of highly variable net water exchanges that must be very carefully measured over long periods of time. The back of the envelope calculation did not deal directly with the exchange at the mouth but focused instead on the rate of storage of N and P within the system. The difficult part of that calculation is properly area and mass weighting the N and P composition of the sediment over a large area and properly estimating the mass of sediment accumulating. As more resources were invested in the budget, the better constrained the numbers became. But the budget framework helped to identify and highlight problems, focus efforts to get the model right, and provide evidence that nutrient load reductions would have desired effects.

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FISHERIES IN LAGOON-ESTUARINE ECOSYSTEMS

Daniel Pauly and Alejandro Yáñez-Arancibia

In this chapter, we review the ''four factors''—recruitment, growth, natural mortality, and fishing mortality—viewed in classical fish dynamics as needed for predicting future from present stock sizes—in the context of lagoon-estuarine fisheries, and discuss the connection between fish catches, community dynamics, and ecosystem functioning. We compare worldwide catches from lagoon-estuarine systems and briefly discuss their management with emphasis on the *bordigue*, a form of tidal trap used in the western Mediterranean area to harvest fish previously recruited to a lagoon and/or to retain undersized fish for another growth cycle. This form of harvest/management, which requires complex social arrangements, may, short of aquaculture, represent the optimum way of using lagoon-estuarine ecosystems to produce fish.

18.1 INTRODUCTION

We briefly review the factors that determine fisheries yield in coastal lagoons, which have been defined by Ardizzone et al. (1988) as ''bodies of water (from low brackish to hyper saline) partially separated from an adjacent sea by barriers of sand or other sediment, with openings through which seawater can flow''.

See Kjerfve (1994) for other definitions, and Day and Yáñez-Arancibia (1982) for an ecosystem-based definition of coastal lagoons and estuaries. ''Fisheries'' refers to the catching of fish and aquatic invertebrates and, hence, excludes aquaculture. When we refer to coastal lagoons, we generally mean coastal and estuarine systems in general. The literature on lagoon-estuarine ecosystems is immense; that on lagoon fisheries is also too large for a balanced review to fit into the space available for this chapter, even after aquaculture is excluded. We, therefore, concentrate on a few themes that we think are of special relevance to lagoon fisheries, yield prediction and management, and to fishes only. Our examples focus on one lagoon-estuarine ecosystem of the Gulf of Mexico and on West African and Mediterranean lagoons. We chose the first two locations because we worked there; and the Mediterranean case because this is where the management scheme emerged that we would like to point out to the readers. Except for a few references, we do not cover the important lagoon fisheries of the Indo-Pacific area. These lagoons are included, however, in the compilation of lagoon fisheries catches discussed in the following section. This chapter builds on the fisheries chapter in the first edition of Estuarine Ecology, and readers are encouraged to refer to that chapter also.

18.2 FISHERIES CATCHES FROM COASTAL LAGOONS

Kapetsky (1984) is still the reference that presents the largest data set on catches from coastal lagoons and compares these with catches from other exploited marine and fresh water ecosystems. As can be seen from Table 18.1, coastal lagoons are, overall, more productive than other ecosystems in terms of fisheries yield, whether one uses the mean or the median as a measure of central tendency. This can ultimately be accounted for by the generally high primary production in coastal lagoons (Nixon, 1982, 1988), for which three reasons may be suggested: (i) Availability of organic matter inputs via rivers (Kapetsky, 1984; Caddy and Sharp, 1986; Deegan et al., 1986; Yáñez-Arancibia et al., 1985a,1985b; Yáñez-Arancibia and Aguirre-León, 1988; Day et al., 1997; Laffaille et al., 1998; Bianchi et al., 1999; Sánchez-Gil et al., 2008); (ii) Shallowness, conducive to rapid remobilization of nutrients (Qasim, 1973a; 1973b; Jones, 1982; Nixon, 1982; Quignard, 1984; Deegan et al., 1994, 2000; Deegan, 2002); and (iii) Velocity and volume of water exchanges between the sea and the estuarine system, which also directly affects fish production via recruitment (e.g., Bourquard and Quingnard, 1984; Caddy and Sharp, 1986; Deegan et al., 1986; Yáñez-Arancibia, 2005; Yáñez-Arancibia et al., 2007).

However, coastal lagoons do not have uniformly high yields and, indeed, the frequency distribution of Kapetsky's yield data is strongly skewed (Fig. 18.1). Some factors leading to this nearly log-normal distribution are, with regard to the numerous occurrences of unproductive lagoons:

1. Extreme salinity and temperature fluctuations, turbidity, anoxic conditions, or toxic discharges (Gunter, 1967).

2. Very shallow sills, preventing sufficient recruitment.
3. Excessive illumination or turbidity, both of which can lead to reduced primary productivity (Qasim, 1973a, 1973b).
4. Lack of sufficient fishing effort (Quignard, 1984; Bailey, 1988), a condition that is increasingly rare.

The few extremely productive lagoons in Figure 18.1 may benefit, on the other hand, from a number of positive factors:

5. A coastal habitat supplying a large recruitment (Pauly, 1986b).
6. Fertilization from rivers and via agricultural runoff, or human sewage and through water exchanges with the sea.
7. A management regime that makes the best of the incoming recruitment.

18.3 FISH POPULATION DYNAMICS AND ITS FOUR FACTORS

18.3.1 Russel's Axiom

The definition of ''fisheries'' in the introduction implies the need for management, because common-property, open-access natural resources systems, given competing users, cannot produce high, sustained yields if left to themselves (Hardin, 1968).

Fishery science and especially its ''operational'' subdiscipline, fish population dynamics, are often articulated by means of Russel's axiom, that is:

$$B_2 = B_1(R' + G') - (M' + F') \qquad (18.1)$$

which states that a well-defined stock (= population) of fish biomass (B_1) will have after an arbitrary period Δt, the biomass B_2 as a result of positive processes (R' = recruitment; G' = growth) having added to the stock, while negative processes (M' = natural mortality; F' = fishery catches) have reduced it (Russel, 1931; Ricker, 1975).

Equation 18.1 does not have a form allowing its direct use for assessment, and hence, this equation is generally used only for defining a problem, as done here. On the other hand, the four processes included in the equation, plus some peripheral processes also considered by fishery biologists (Fig. 18.2), have been put in a mathematically tractable form (Schaefer, 1957; Beverton and Holt, 1957; Ricker, 1954, 1975; Gulland, 1983; Pauly, 1984, 1998; Hilborn and Walters, 1992). In this chapter, we present a few of the models that

TABLE 18.1 Fisheries yields of coastal lagoons (all groups included) as compared with the yields of other aquatic ecosystems

Systems	Yields (t/km²/year) Median	Mean	n
Coastal lagoons	5.1	11.3	107
Continental shelves	4.8	5.9	20
African/Asian reservoirs	4.2	7.5	41
Coral reefs	4.1	4.9	15
River floodplains	3.2	4.0	33
Reservoirs (United States)	1.3	2.4	148
Natural lakes	0.5	2.8	43

Source: From Kapetsky (1984).
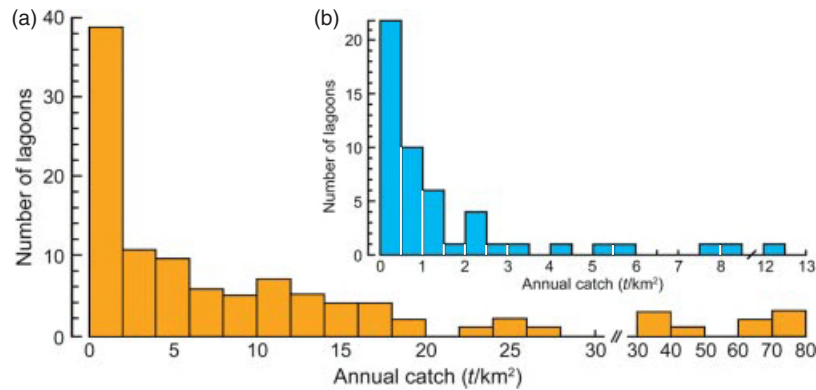
FIGURE 18.1 Frequency distribution of fishery catches from coastal lagoons. *Source:* From Kapetsky (1984). (a) Finfish, $n = 106$. (b) Penaeid shrimp, $n = 51$.
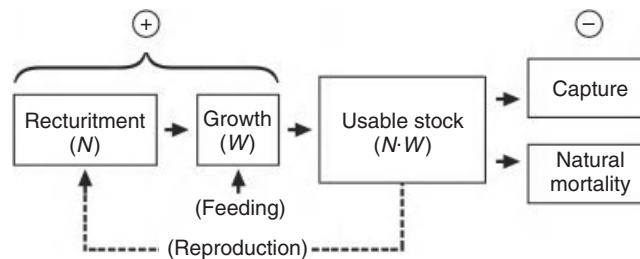
FIGURE 18.2 Schematic representation of four key factors determining the future biomass of and catches from a stock: Recruitment where $N =$ number of fish added to the stock, individual growth in weight (W) of the fish recruited into the usable stock, natural mortality, and capture via fishing mortality. Feeding and reproduction, although necessary for stock build up and maintenance, are usually not part of classical fish population dynamics. *Source:* Adapted from Russel (1931) and Ricker (1975).

have resulted from these efforts, specifically those that have been used in dealing with lagoon-estuarine systems. The four factors shall be examined in the sequence: growth, natural mortality, fishing mortality, and related factors (mainly catch/effort), with recruitment being last, because it is the most complex factor to investigate, model, and predict.

18.3.2 Growth of Fishes in Lagoon-Estuarine Systems

Lagoon environments are highly seasonal, more so than the open marine environment to which they are connected. Thus, the food types (Aguirre-Leon and Yañez-Arancibia, 1986; Chavance et al., 1984; Fig. 18.3) and food consumption, and hence, the growth of lagoon fishes are bound to oscillate seasonally, whether the fish in question undertake seasonal migrations in and out of coastal lagoons or not. Another, perhaps the dominant, source of seasonal oscillations is water temperature, which exerts a profound influence on the metabolic processes of poikilotherms and hence on their growth (Pauly, 2010).
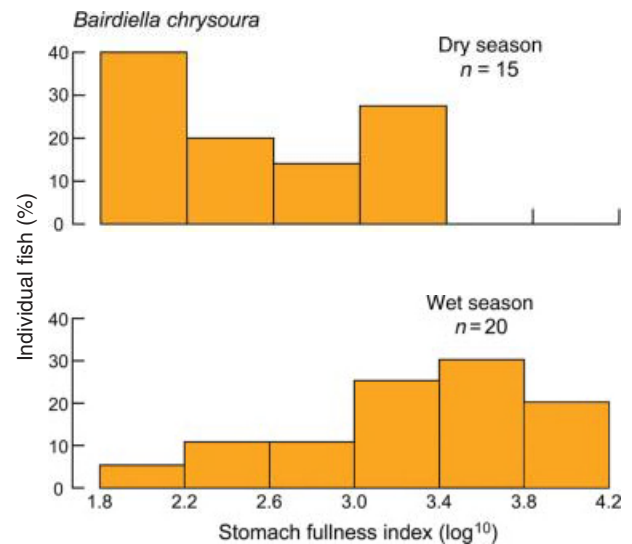
FIGURE 18.3 An example of seasonal changes in the stomach contents and hence, presumably the food consumption of a lagoon fish, the silver perch *Bairdiella chrysoura*, Terminos Lagoon, Mexico. *Source:* Adapted from data in Chavance et al. (1984).
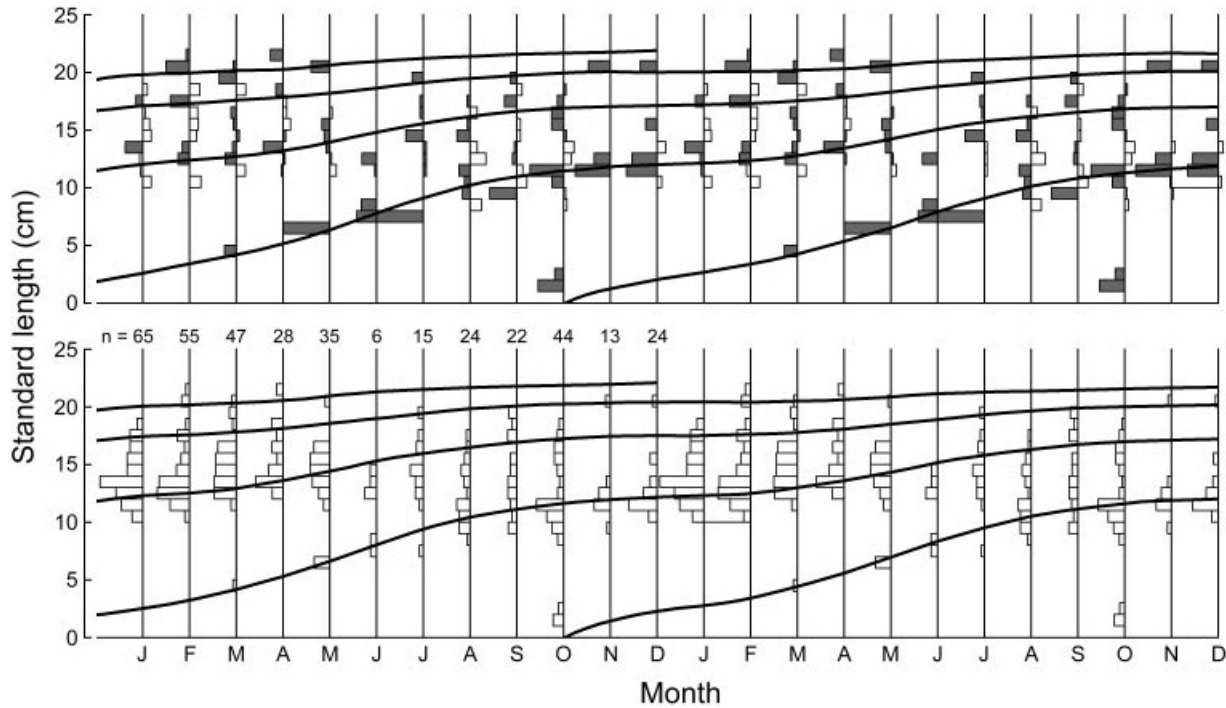
FIGURE 18.4 Seasonal growth of the checkered puffer *Sphoeroides testudineus* (Tetraodondidae) from Biscayne Bay, Florida, based on length frequency data from Targett (1979; lower panel). Note ''doubling up'' of the data set, and sample sizes ($n = 65$, 55, etc.). The upper panel shows the ''restructured'' length frequency data, as used internally by the ELEFAN program of Pauly and David (1981). *Source:* Adapted from Pauly and Ingles (1981).

Various authors have modified the von Bertalanffy equation (Bertalanffy, 1938), commonly used to express growth of fish, to accommodate seasonal growth oscillations (see e.g., Longhurst and Pauly, 1987; Hoenig and Chaudhury Hanumara, 1982; Soriano and Jarre, 1988; Pauly, 2010).

Figure 18.4 presents an application example pertaining to a puffer fish displaying weak seasonal growth oscillations, as is often the case in tropical and subtropical waters (Pauly and Ingles, 1981; Longhurst and Pauly, 1987). The growth models presented by the authors above can accommodate stronger growth oscillations, all the way up to a very short period of zero growth, for example, when temperatures are lowest (Pauly, 2010). However, these models cannot accommodate longer periods of zero growth. Therefore, we used a model that can accommodate a (''winter'') period of growth stagnation called *no-growth time* (NGT; Pauly et al., 1992). To fit such a curve, the time axis is divided into one growth and one NGT over each period of one year. Then, during growth time, we have

$$L_t = L_\infty[1 - \exp(-w)], \quad (18.2)$$

in which L_t is the length at age t, and where

$$\omega = K(t' - t_0) + \frac{\dfrac{K}{2\pi}}{(1 - \text{NGT})} \left[\sin \frac{2\pi}{1 - \text{NGT}}(t' - t_s) - \sin \frac{2\pi}{1 - \text{NGT}}(t_0 - t_s)\right], \quad (18.3)$$

where t' is obtained by subtracting the total amount of NGT that the fish experienced from the age t, since $t = 0$.

The other parameters are L_∞ the asymptotic length, that is, the average length the fish would attain if they lived indefinitely; K, twice is the parameter expressing how fast L_∞ is approached, t_0 is the theoretical ''age'' at length zero if the fish always grew according to the equation, and t_s is the parameter adjusting a seasonal cycle to start at $t = 0$. Note that the seasonal growth itself (outside of *NGT)* is described by a sine wave curve with period $1 - \text{NGT}$, and that the unit of K' is $(\text{year} - \text{NGT})^{-l}$ instead of year^{-l}.

An application example for this model is given in Figure 18.5. As might be seen, the model predicts a no-growth time of about three months (January to March) for the European seabass (*Dicentrarchus*
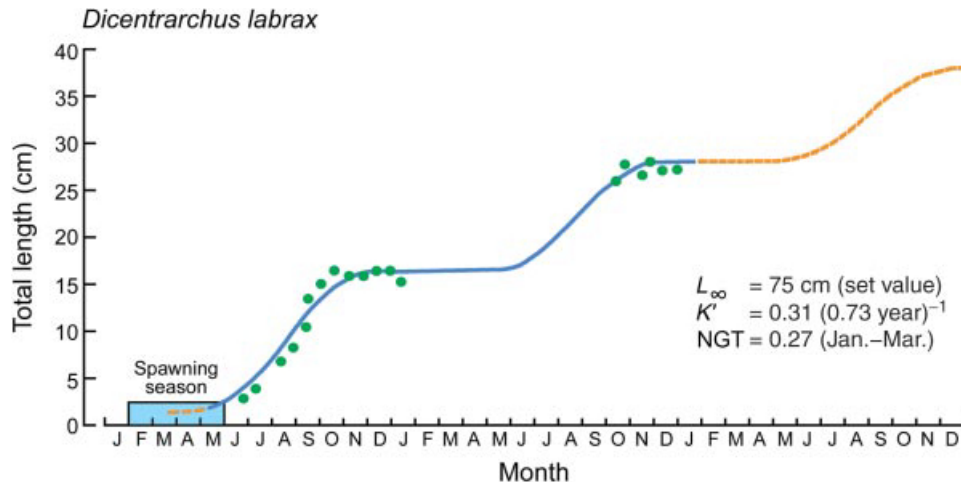
FIGURE 18.5 Seasonally oscillating growth of a European sea bass, important in Mediterranean lagoon catches. *Source:* Monthly size data from Quignard (1984); maximum size ($\approx L_\infty$) and spawning season from Beauchot (1987).

labrax) in l'Etang d'Or, France, a feature that other seasonal growth models could not have picked up.

When growth is not seasonal, that is, when one deals with data points that are one year apart or when working with otolith microstructures of fish not belonging to a given cohort, the standard (non-seasonal) von Bertalanffy curve can be used. It has the form:

$$L_t = L_\infty(1 - e^{K(t-t_0)}), \tag{18.4}$$

where L_∞ and t_0 have the same definitions as in Equations 18.2 and 18.3, where K has the dimension of time^{-1} (e.g., year^{-1}). An application example is presented in Figure 18.6.

The growth of fishes within coastal lagoons relative to that of conspecifics growing in other habitats appears to be a function of (i) the type of lagoon and/or of habitats being compared, (ii) the species of fish, and (iii) the life stage of the fish species.

Thus, Chauvet (1988) suggests that shallow, eutrophic lagoons lead to improved growth compared with that in deep lagoons, strongly influenced by the marine regime. He also noted, with regard to Mediterranean species such as gilthead sea bream (*Sparus aurata*) and European sea bass, that the lagoon habitat appears to lead to higher growth rates among the juveniles and young adults (Fig. 18.7), while among the larger, older specimens of these two species, growth within lagoons is at best equivalent to, and generally less than, that in the marine environment (Chauvet, 1988).

The West African coast offers further and clearer indications of at least small coastal lagoons being habitats, leading, independently of fishing effects, to
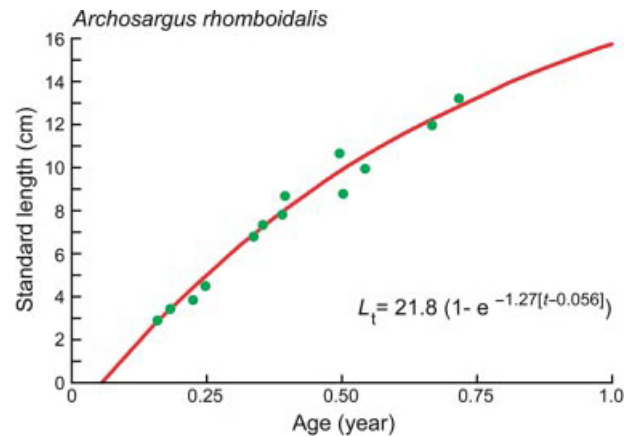
FIGURE 18.6 Growth of Western Atlantic sea bream *Archosargus rhomboidalis* (Sparidae) in Terminos Lagoon, Mexico, as inferred from counts of otolith microstructures (recomputed from Chavance et al., 1986). The new parameter estimates derived here differ from those originally presented because a nonlinear routine was used to fit the data: the new estimation of $L_\infty = 22$ cm is closer to the maximum length in Terminos Lagoon (23 cm) than the original estimated $L_\infty = 20$ cm. *Source:* Adapted from Chavance et al. (1986).

reduced final (maximum) sizes among resident fishes: (i) the maximum observed size of the blackchin tilapia *Sarotherodon melanotheron* (Cichlidae) in the small poikilohaline Sakumo Lagoon was 19.5 cm (Pauly, 1976) versus 25 cm in the much larger estuarine Lagos lagoon (Fagade, 1974), and (ii) the two forms of the "bonga" *Ethmalosa fimbriata* (Clupeidae) appear to occur in West Africa, one occurring along the coast, and in estuaries and large "open" coastal lagoons, and reaching sizes of up to 30 cm, and the other
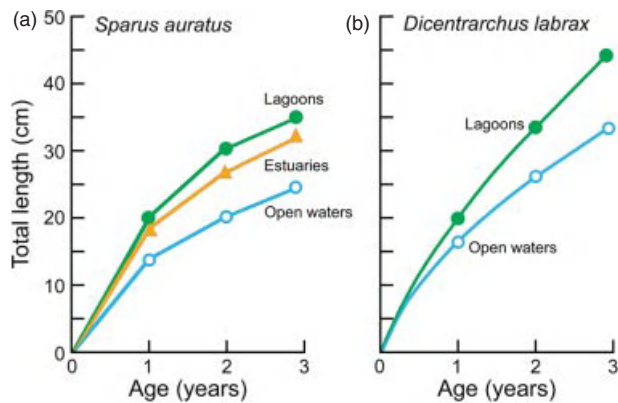
FIGURE 18.7 Growth differences among juveniles of two species of fishes important to Mediterranean lagoon fisheries. (a) Gilthead sea bream. (b) European sea bass. Note improved growth in the lagoon habitat. *Source:* Adapted from Chauvet (1984, 1988).

limited to a length of about 15 cm and occurring and reproducing only within closed lagoons (Longhurst and Pauly, 1987). Note that these effects are independent of, and added to, the size-based artificial selection that is imposed by a long-term fishery, and which ultimately results in small adults (Conover and Munch, 2002; see also Pauly (2002) for the case of *S. melanotheron*).

Improved growth of juveniles and limited maximum sizes of adults are not necessarily incompatible. Indeed, rapid juvenile growth due to availability of abundant food and high habitat temperatures generally implies a reduction of maximum adult sizes. Longhurst and Pauly (1987) give reasons, amplified in Pauly (2010), why this should be so.

18.3.3 Natural Mortality of Fishes in Coastal Lagoons

The natural mortality of a fish population is straightforward and can be modeled using:

$$N_2 = N_1 e^{-M\Delta t}, \qquad (18.5)$$

where N_1 and N_2 are the numbers of fish at the beginning and end respectively and M is the instantaneous rate of natural mortality during a period Δt. Instantaneous rates such as in Equation 18.5, for example, natural (M) and fishing (F) mortality, can be added to yield the total mortality (Z) and the latter used in equations analogous to Equation 18.5.

Beverton and Holt (1959) were the first to demonstrate rigorously that the growth performance of fishes is strongly correlated with their natural mortality, that is, that the growth parameter K of fishes with similar L_∞ values (Eq. 18.4) generally remains close to a constant proportion of M. Their findings were generalized by Pauly (1980) based on data from 175 fish stocks to yield the empirical equation:

$$M \approx (K^{0.65}) \frac{T^{0.46}}{L_\infty^{0.28}}, \qquad (18.6)$$

where L_∞ is the asymptotic length (total length, in centimeters), K is per year, and T the environmental temperature in degree Celsius.

Hence, lagoon fishes, which tend to have higher K and lower L_∞ values than their conspecifics in open waters, can be expected to have generally higher natural mortalities than their open-water counterparts. This explains the observation of Chauvet (1988), who noted that "strangely, it is in the lagoon habitats that are most favorable for growth that the mortality rates are highest . . ."

It is important, however, to distinguish between the relatively low natural mortality rates affecting late juveniles and adults, which are fairly constant and largely predictable, from those affecting larval and early juveniles, which are high and essentially unpredictable.

Moreover, an important distinction with regard to lagoons is that between natural mortality rates as discussed above and catastrophic mortalities, as caused, for example, by dystrophic crises (Chauvet, 1988). The former may be seen, at least as far as populations rather than individuals are concerned, as a gradual process. Thus, natural mortality, as influenced or determined by predation, will be more or less continuous over a certain period and can be compensated for by population growth, leading to the observed narrow range of M/K values. Otherwise, populations could not maintain themselves over evolutionary timescales.

Catastrophic mortalities, on the other hand, which are quite frequent in lagoon-estuarine systems, are episodic events, usually connected with sudden changes of water characteristics such as dissolved O_2, H_2S content, and temperature, which can induce large-scale death among resident stocks and sometimes their total annihilation.

Many natural or anthropogenic factors may cause catastrophic mortalities in coastal lagoons, including the following:

1. Eutrophication, leading to nighttime depletion of oxygen and/or benthic production of H_2S, which can be released into the water column by storms.

2. Cold or hot spells, particularly effective in shallow lagoons (Gunter, 1952, 1957, 1967).

3. Terrigenous pollution, for example, from agricultural pesticides.

Catastrophic mortalities are difficult to incorporate into standard population dynamics models and have indeed not generally been considered explicitly in fisheries management. Their probability of occurrence and their prevention are, however, important aspects of management schemes involving *bordigues* and aquaculture in coastal lagoons.

18.3.4 Fishing Mortality and Related Statistics

Fishing mortality defined above as $F = Z - M$ can also be defined as follows:

$$F = \frac{C}{B}, \tag{18.7}$$

where C is the fisheries catch (in weight) during a given period and B is the mean biomass during that same period. Equation 18.6 provides the rationale for attempts to estimate the biomass of fishes in coastal lagoons using, for example, tagging (Lam and Lasserre, 1984). Given Equation 18.7, we also have

$$C = q \cdot f \cdot B, \tag{18.8}$$

where f represents the fishing effort and q is the catchability coefficient of the gear used to generate the level of effort f. These definitions imply that C/f (the catch per unit of effort or CPUE) is, given a constant q, proportional to the biomass and hence can be used to monitor the status of a stock whose absolute biomass may be unknown (Fig. 18.8a).

Lam and Lasserre (1984) reviewed the applicability of these and related models, notably yield-per-recruit (Y/R) and cohort analysis, to lagoon fisheries, and the methods, for example, surveys or tagging studies, used to estimate their parameters. Their conclusions were as follows:

1. The assumption of equilibrium implicit in most standard models for analyzing the population dynamics of fish (notably Y/R analysis) render these models questionable when applied to data from lagoon fisheries.

2. The scattered and often small-scale nature of fisheries operation in coastal lagoons generally makes the routine collection of C/f data too costly. Hence, such data are lacking for most lagoons (Kapetsky, 1984) or are largely unreliable (Bailey, 1988).

3. The methods that may be most appropriate for lagoon fisheries, that is, virtual population analysis or cohort analysis (Gulland, 1965; Pope, 1972), which have the advantage of not requiring estimates of fishing effort, do require catch-at-age data, which can be obtained in a cost-effective
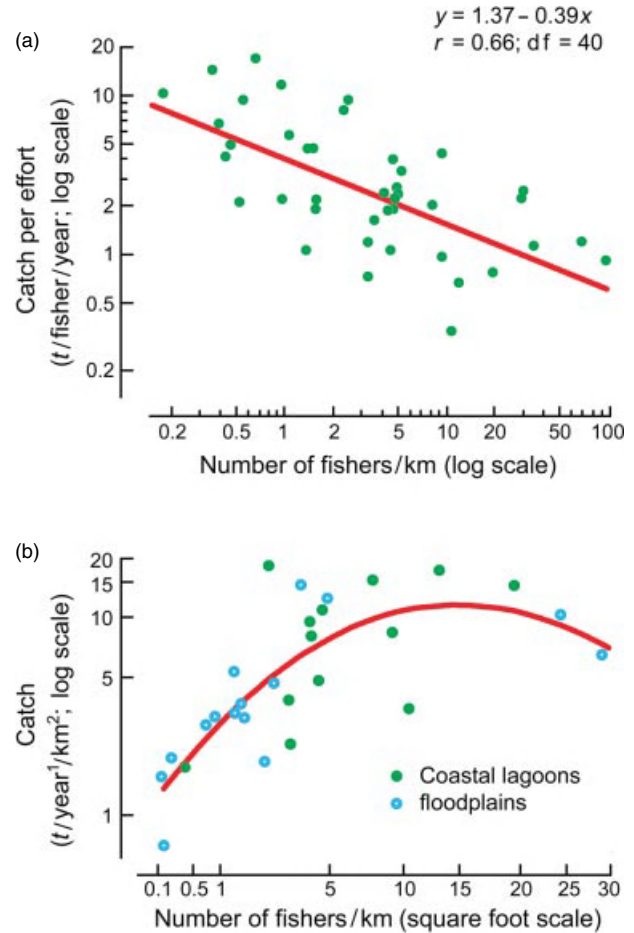
FIGURE 18.8 Examples of the relationship between fishing effort per area, that is, fishing intensity, and dependent variables. (a) Relationship between C/f and fishing intensity in 42 coastal lagoons (Kapetsky, 1984). (b) Relationship between yield, C, and fishing intensity in 13 coastal lagoons and 15 river floodplains, which appear to have similar yield. *Source:* After Bailey (1988).

manner only for the most important species in major lagoon fisheries.

4. It may be most appropriate to manage lagoon fisheries as a black-box system, using a form of adaptive management in which the catches resulting from initial interventions are monitored and used to refine the next set of interventions.

Bailey (1988), working on various tropical small-scale fisheries data sets, including coastal lagoons, noted that the inclusion of fishing effort added considerably to the precision of empirical (i.e., black-box) models in predicting yields in such systems. He derived, for lagoons $(n = 13)$ and floodplains $(n = 15)$,

the joint model (Fig. 18.8b):

$$\log_e(\text{yield} + 1) = -0.19 + 1.44f^{0.5} - 0.19f \quad (18.9)$$

for an annual yield expressed in tons per square kilometer, and where f is the fishing effort per area (here, fishers per square kilometer of lagoon or floodplain area). This model has an intercept unequal to zero and, hence, predicts a nonzero yield where $f = 0$. It should not be used with small values of f (Bailey, 1988).

While pleased with the predictive power of his model, given the heterogeneity of the available data set (Kapetsky, 1984), Bailey (1988) also noted that external approaches such as his may have reached a dead-end, not because of their empirical nature, but because of the lack of acceptable data ''in terms of number of systems and quantity of variables measured consistently'' and that this type of approach may thus ''have reached an impasse with respect to prediction of future size of stocks or yield.''

While based on different premises, this conclusion echoes that of Lam and Lasserre (1984). The application of classical methods of fish population dynamics and fishing management to coastal lagoon fisheries appears inappropriate, even if isolated elements of lagoon resource systems can be described by these classical methods.

18.3.5 Recruitment of Fish Stocks in Lagoon-Estuarine Systems

18.3.5.1 The Fishery Approach toward Recruitment

Providing reliable predictions of the recruitment of a fish stock for use in fishery management is something that has largely eluded fishery biologists, despite massive efforts being put in since the very beginning of fishery science as a discipline of its own near the end of the last century (Pauly, 1986a). Classical population dynamics, as formulated in the text of Beverton and Holt (1957) or Ricker (1958), resolved this problem by combining the basic processes presented above into models for predicting yield per recruit as a function of the control variable such as F and age at first capture (t_c). An example of such model is as follows:

$$\frac{Y}{R} = F \cdot e^{Mr2}W_\infty \left[\frac{1}{Z} - \frac{3e^{-Kr_1}}{Z + K} + \frac{3e^{-2Kr_1}}{Z + 2K} + \frac{e^{-3Kr_1}}{Z + 3K} \right],$$
$$(18.10)$$

where $r_1 = t_c - t_0$ and $r_2 = t_c - t_r$, Z and K are as defined above, W_∞ is the weight corresponding to L_∞, and recruits of age t_r are defined as fully metamorphosed young fish whose growth is described

adequately by an equation also describing the growth of the adults, whose instantaneous rate of natural mortality is similar to that of the adults, and who occur in or swim into some fishing ground (Pauly, 1984, 1994).

Following Ricker (1954), numerous fishery biologists have attempted to develop models linking the parent stock and the subsequent recruitment. The various curves resulting from these efforts have not been reviewed here (but see Sharp and Csirke, 1983).

18.3.5.2 The Ecosystem Approach toward Recruitment

Ecological implications of recruitment in functional structures of estuarine and coastal fish communities, and implications to fisheries in coastal lagoons and estuaries are key concerns toward ecosystem-based management of coastal fisheries in the Gulf of Mexico and elsewhere.

Three groups of fishes occur in coastal lagoons: (i) sedentary species: those which spend their entire life cycles within coastal lagoons; (ii) seasonal migrants: those which enter the lagoon during a more or less well-defined season from either the marine or the fresh water side and leave it during another season (Fig. 18.9); and (iii) occasional visitors: those which enter and leave a lagoon without a clear pattern within and among years. Group (i) is usually very limited, especially when species with planktonic stages are considered. Most lagoon fishes spawn outside lagoons. The above-mentioned black chin tilapia, a male mouth brooder, is an exception and its special ability to withstand large variations of temperature and salinity has enabled it to dominate the fauna of small closed lagoons completely along the West African coast (Pauly, 1976).

Generally, however, it is the members of group (ii) that dominate the fauna of coastal lagoons, for example, by contributing near 100% of the ichthyofauna of many Mediterranean lagoons (Quignard, 1984). Group (iii) is represented in the Mediterranean by species such as the garfish *Belone belone* or the Atlantic mackerel *Scomber scombrus* (J.P. Quignard, personal communication), by species such as snapper *Lutjanus* spp. or crevalle jack *Caranx hippo* in West African lagoons (Pauly, 1975), or species such as gafftopsail sea catfish *Bagre marinus*, Atlantic anchoveta *Cetengraulis edentulus*, Western Atlantic sea bream *Archosargus rhomboidalis* or tomtate grunt *Haemulon aurolineatum* in lagoons of the southern Gulf of Mexico (Fig. 18.9).

To these three basic groups, two other groups may be added (iv) marine, estuarine-related species, which spend their entire life cycle in the upper shelf under
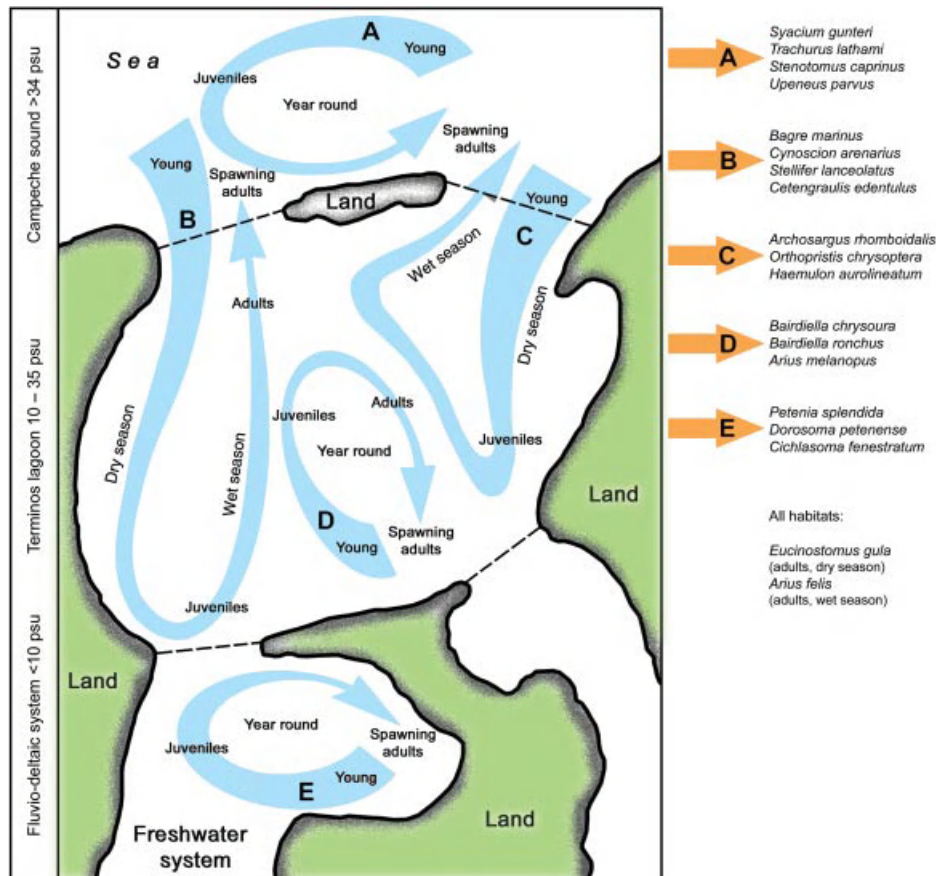
FIGURE 18.9 Examples of fishes with characteristic migration pattern within, outside of, and into and out of Terminos Lagoon, Southern Gulf of Mexico. *Source:* Redrawn from Yañez-Arancibia et al. (1988); Yañez-Arancibia and Sanchez-Gil (1988); Sanchez-Gil and Yañez-Arancibia (1997).

the influence of an estuarine plume, for example, fringed flounder *Etropus crossotus*, shoal flounder *Syacium gunteri*, and rough scad *Trachurus lathami* (Sanchez-Gil and Yañez-Arancibia, 1997; Sanchez-Gil et al., 2008); and (v) fresh water, estuarine-related species, which spend their entire life cycle in the fluvial-deltaic zone in the upper reaches of estuarine systems, for example, *Petenia* spp. and *Cichlasoma* spp (Yañez-Arancibia et al., 1993, 1994).

Different opinions exist with regard to the mechanisms of recruitment into lagoons of group (ii) fishes. Quignard (1984) and Chauvet (1988), representing the ''Eastern Atlantic school,'' stress that the recruitment of group (ii) fishes into coastal lagoons is not necessarily due to migrations (Harden-Jones, 1968). Rather, fishes of this group are either flushed into lagoons while still in the planktonic stage, or swim as early juveniles into lagoons against the outgoing current, either due to their effort to stay close inshore or due to coastal wanderings (*errances* in French texts) in search of food.

The other school, which may be called ''Western Atlantic,'' stresses on the important role that lagoons play in the life cycles of many coastal fishes. Here, lagoons are viewed as major elements of small-scale migrations, which, by involving lagoon/estuarine habitats, allow a high standing stock to be maintained (Fig. 18.10).

In either case, the relative level of recruitment into coastal lagoons will be determined between lagoons by the ease with which fish can penetrate into these and between years by the overall number of potential recruits along the coast. The former point implies, as also emphasized by Chauvet (1988), that recruitment to coastal lagoons can be artificially increased by keeping the mouth of lagoons open during periods when juveniles of preferred species occur along the coast, or by deepening the sill of lagoons with very shallow mouths.

Coping with between-year variability of recruitment to lagoons is more difficult, and one of the

(a)

Small- scale migrations
Catadromous Anadromous

(b)

Large-scaie migrations
Anadromous
Juveniles
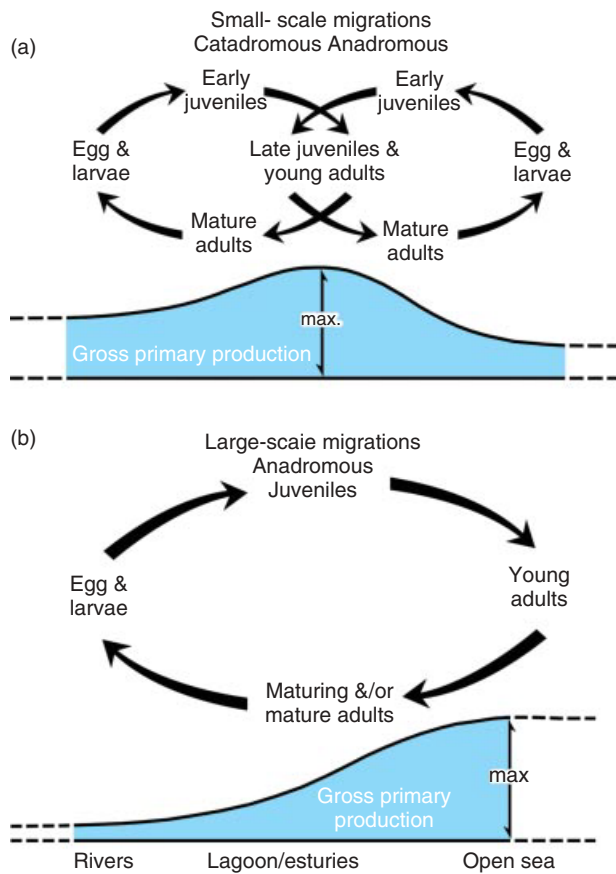
FIGURE 18.10 Schematic representation of (a) small-scale migrations involving shelf, lagoon/estuary, and fresh water habitats and allowing certain tropical fish stocks to maintain higher abundance than if they utilized only one type of habitat, and (b) large-scale migration. Note the marked difference of the scheme in (a) to the cold/temperate situation, characterized by large-scale anadromous migration. *Source:* After Yañez-Arancibia and Sanchez-Gil (1988).

few practical approaches for dealing with this problem is management through bordigues, the gear and management tool to which the Food and Agriculture Organization of the United Nations (FAO) has devoted its first manual on lagoon management (Chauvet, 1984).

18.4 MANAGEMENT OF LAGOON-ESTUARINE FISHERIES

18.4.1 Conventional Fisheries Management

As alluded to in the introduction to this chapter, fisheries, at least in modern times, tend to quickly

become overfished unless they are well managed, the result of an overwhelming harvesting capability applied to finite resources that belong to no one before they are caught (common property) and which everyone has the right to exploit (open access). Fisheries management, therefore, generally involves putting restrictions on (i) access to the resources, (ii) number of gears, (iii) type of gear deployed, (iv) timing of effort deployment, or (v) some combination of these (Pauly et al., 2002). The models used to derive the numbers needed for such management are commonly analytical models (Beverton and Holt, 1957), or surplus-production models (Schaefer, 1957), with either of these possibly containing some economic component, that is, consideration of fishing costs and gross returns.

One commonly used analytic model, structured around the four factors discussed above, is the yield-per-recruit model (Eq. 18.9), which can be used to assess the optimum size/age at first capture. The optimum mesh size in a given fishery with known fishing mortality identifies the optimum fishing mortality, given a certain unique range of size/age at which the fish of a given stock should be caught. Such computations can be made more realistic by adding a size–value relation into the model, which leads to optimum monetary or nonmonetary return per recruit being evaluated (Die et al., 1988).

Surplus-production models, on the other hand, can either be time- or space structured. In the former, a time series of catch data from a given fishery is related to the corresponding time series of effort data such that the optimum level of effort, yielding the largest (hopefully) sustained catch (maximum sustained yield or MSY) is identified (Schaefer, 1957; Ricker, 1975). The other class of surplus-production model is based on the assumption that a number of units compared, such as lakes, lagoons, and coastal stretches, had similar potential production before onset of a fishery and that catch differences between them are due to different levels of effort (Munro, 1979). This leads to models such as Equation 18.8, which allow rough estimation of potential or optimum yields for given levels of effort. This allows the assessment of whether a lagoon is under- or overfished. Unfortunately, long time series of catch and effort data, needed for fitting time-structured surplus models, are generally lacking for lagoon-estuarine systems.

Yield-per-recruit models, on the other hand, when thoughtlessly used to assess fishes or shrimp stocks within lagoons, tend to lead to the same results: wherever they are applied, they suggest that it is better to let the generally small fish and shrimp that occur inside lagoons escape, and be caught later

by some offshore fishery. This reflects the fact that, until recently, fishery research viewed lagoons as one side of an antagonistic relationship, in which often poor, small-scale fishers catch large numbers of undersized fish and shrimp, which if they had escaped from the lagoons, would have contributed yields to the (usually industrial) fisheries outside the lagoons (Garcia and Le Reste, 1981). There exists, however, an approach by which the conflict between lagoon and coastal fisheries can be resolved, and this involves turning coastal lagoons from marginal sites for harvesting of undersized fish into production units making the most of the natural recruitment they receive, just as any well-managed coastal fishery is supposed to do.

18.4.2 Using ''Bordigues'' As a Tool for Lagoon-Estuarine Fisheries Management

The French word ''bordigue'' (from the Provencal *bourdigo)* refers to a fishing gear widespread around the Mediterranean and representing the culmination of an evolution spanning over two millennia (Chauvet, 1988; McCann, 1988). It is essentially a trap, and its basic principle is simple: all young fish attempting to get into the lagoon through a bordigue can, but those who try to leave the lagoon cannot (Fig. 18.11). Bordigues, which are usually placed along the channel connecting a lagoon and the sea, thus differ in principle from gears such as traps, fish corrals, and gill nets that are often deployed in great numbers within the lagoon, but without totally blocking the outlet, and which hence let a fraction of the fish leave the lagoon to the sea.

Here, the question might arise how can a gear that retains all the fish attempting to leave a lagoon be useful to management? The point is that the bordigues are constructed so that the fish they retain are not killed, but rather graded according to size, and diverted into holding pens through adjustable panels of different mesh sizes. Only fish that have reached market size are harvested. The others are returned to the lagoon to grow until the next harvest season along with fresh recruits that have just entered the lagoon. Figure 18.12 contrasts the operation of a bordigue over a period of several years after being set up with the traditional exploitation scheme of a lagoon, as repeated every year.

As might be seen in Figure 18.12a, the harvest of a conventionally managed lagoon will be based only on the single recruitment event preceding it, there being no fish left in the lagoon from previous recruitment. Thus, catches will vary between years as a function of recruitment levels, given consistent effort, and the fish caught will be of low sizes.

Bordigues, on the other hand, lead to a harvest level that is a function of the average level of recruitment over several years, besides harvesting fishes that are always of optimum size. Thus, bordigues allow the kind of resource exploitation that is optimal in terms of yield-per-recruit analysis, where fish that have not grown to sufficient size escape through the mesh of the gear, grow some more, and then may be caught, or again escape through the mesh of gear, depending on whether they have grown to some size deemed as optimal in terms of weight or price.

As in a well-managed fishery, the optimum size at harvest in a bordigue will thus depend on the ratio between growth and natural mortality. Therefore, it would make little sense for the small fish retained by a bordigue to be returned to a lagoon in which natural mortalities are such that they offset any gain in individual weight of the released fish. Thus, managing a lagoon by means of a bordigue also implies removing as many sources of natural mortality as possible, for example, by filling in deep pools in which large predators can accumulate, as well as reducing the likelihood of catastrophic mortalities by preventing inflows of pollutants. *Acadja*-type structures within lagoons, which enhance the survival and the growth of young fish, may be considered in this context.

The technical aspects of the construction of bordigues have been discussed in Chauvet (1988). It is worth mentioning that their *construction* requires sophisticated engineering and large investments. However, daunting the technical and financial aspects of the construction of bordigues are, it is social factors that usually prevent their widespread implementation. Notably, the use of bordigues as a fishing gear and management tool requires from those with access to or fishing rights in a lagoon an extremely high degree of cooperation and well-honed management skills. Bordigues must be staffed permanently to prevent them from becoming clogged with drifting sea grass and to change the retaining panels of different mesh sizes depending on which species are in the process of swimming to different retention chambers. Also, fishing within the lagoon must be restrained, as it could otherwise offset the gains obtained by returning undersized fish retained by the *bordigue* to the lagoon. Fishing in lagoons equipped with bordigues (Table 18.2) is not suitable for individualistic fishers. Bourquard and Quignard (1984) document the case of a bordigue that failed because of their noncooperation.

We have not presented the bordigue as a management tool for lagoon fisheries because we
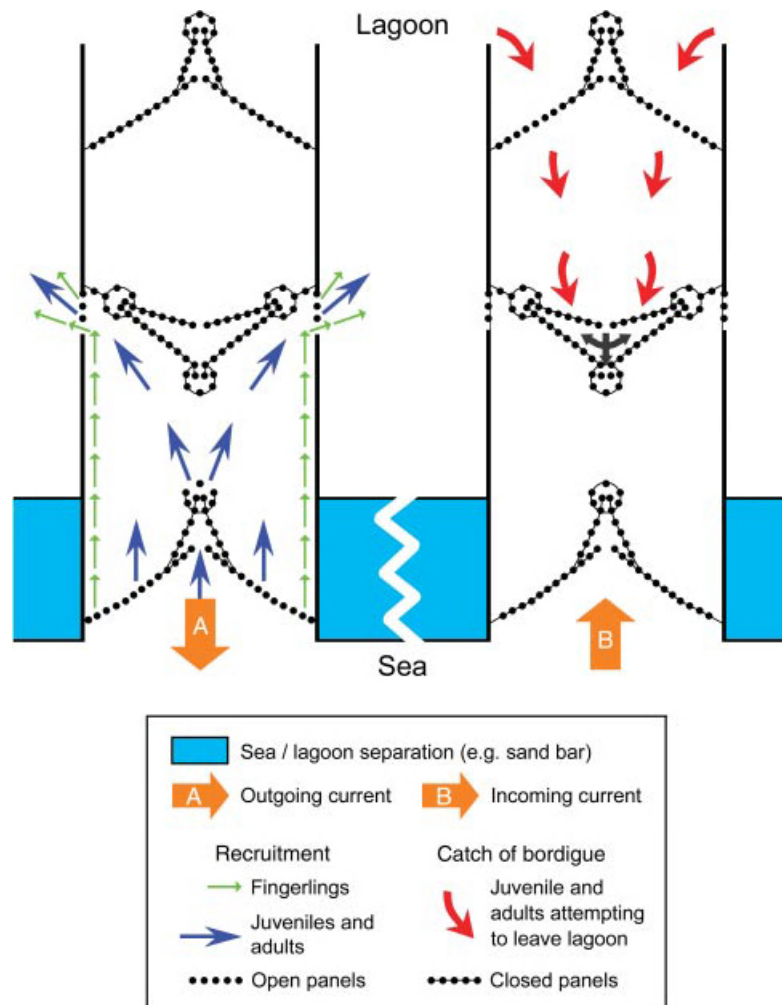
FIGURE 18.11 Schematic representation of a (Tunesian) bordigue, showing (a) how recruits are let through to the lagoon when the water flows out of the lagoon, and (b) how fish attempting to leave when the water flows into the lagoon are caught to be either marketed or returned to the lagoon for another growth cycle. *Source:* After Chauvet (1988).

believe that this method of harvesting and managing is likely to become widely adopted outside its area of origin. We realize that, although it is technically applicable in principle in virtually any place in the world, the potential for its adoption outside the Western Mediterranean is rather low, mainly because of the high degree of cooperation and management skill that is required.

Rather, we have presented the bordigue as an important element in the continuum of lagoon fisheries, which range from totally unmanaged to partially and well-managed fisheries and beyond, to extensive, semi-intensive, and intensive aquaculture operations. Indeed, the bordigue is one of the most sophisticated capture fisheries regime one can imagine. It requires a level of cooperation and of management skill probably higher than that involved in

extensive aquaculture, whose yield the bordigue can approximate (Table 18.2). Other worthwhile management regimes for lagoon-estuarine fisheries do exist and have been discussed by Kapetsky and Lasserre (1984) and Mann (2000); see also the fisheries chapter in Day et al. (1989).

18.5 DISCUSSION

18.5.1 Uncertainty to Understand Fish Resource Dynamics

Fish production in lagoon-estuarine systems is generally high (Day et al., 1989; Yañez-Arancibia et al., 1994, 1993, 1988; Mann, 2000), and this generally leads to high fishery catches. From our experience, one reason
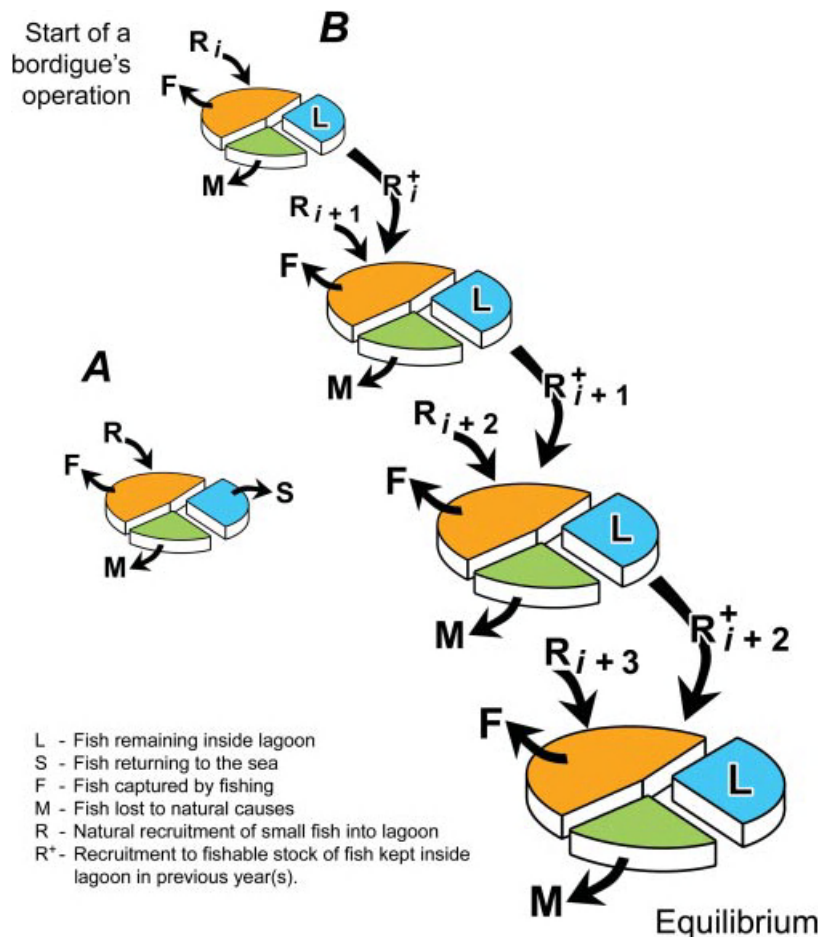
FIGURE 18.12 Schematic representation of differences between (a) a lagoon exploited by gears deployed within the lagoon and (b) a lagoon exploited/managed via a bordigue. Note the buildup of fish biomass within the lagoon in case (b), due to retention of undersized fishes, which would have left the lagoon in case (a). *Source:* After Chauvet (1988).

for this high production is that many of the fish species of importance in lagoon-estuarine environment are either (i) *r*-selected *sensu* (Pianka, 1978), that is, relatively small, fast growing, high production/biomass (P/B) ratio or (ii) the juvelines of *K*-selected species, that is, the fast growing, high production stage fishes whose large adult form, however, typically occurs outside the lagoon. The high P/B ratios of the constituent species are not the only explanation for the generally high production of lagoon-estuarine fish communities. The high biomasses themselves, that is, the high carrying capacities of these ecosystems in terms of seasonal food availability to fishes, also play a crucial role.

In areas where lagoon systems have maintained themselves over long periods (i.e., the Gulf of Mexico), evolutionary mechanisms have emerged that have stabilized and refined such seasonal programming, making the fish population in question gradually

more dependent on the estuarine system for the maintenance of high biomass. In other areas where the lagoon system does not persist or is not regularly open to juvenile migration (i.e., along the coast of Northwestern Africa, the Pacific coast of Mexico, and the eastern coast of East Australia), the use of lagoons seems to be more a matter of random movements along the coast and of inshore movements, that is, *errances*. This implies (i) a lower conversion of primary and secondary production into fish flesh and hence (ii) lower biomasses of coastal fishes. However, the practical difficulties in separating random along-shore/inshore movements, that is, *errances*, from evolutionary fine-tuned, *aimed* movements toward and within estuaries, and the difficulties involved in precise field estimation of biomass and conversion efficiencies, make rigorous testing of the hypothesis difficult. Indeed, this may be the main reason for the continuing debate on the degree of dependence

TABLE 18.2 Comparative fishery yields of lagoons with and without systems to improve survival and/or growth of recruits (Chauvet, 1988)

Location System	Annual Mean^2 Yield, t/km^2	Standard^2 Error, t/km^2	n
Africa	—	—	—
Fishing only	0.10	0.52	10
Acadja^a and fishing	7.75	2.57	3
Mediterranean	—	—	—
Without bordigues^b	0.83	—	52
Nonpermanent bordigues	0.82	0.64	10
Permanent bordigues	1.85	0.18	2
Permanent bordigues plus artificial stocking^c	3.77	2.96	4

^{a}See Kapetsky (1981) for a description of *acadja*-based fisheries.
^{b}Computed by subtracting bordigues yields from grand mean for Mediterranean.
^{c}This is a form of aquaculture (Ardizzone et al., 1988).

of tropical coastal fishes on coastal lagoons and estuaries.

18.5.2 An Unfinished Agenda

Longhurst and Pauly (1987) have pointed out that relatively few finfish and shellfish species are fully adapted to a life cycle within a lagoon-estuarine system *sensu stricto*. Nevertheless, it is clear that in the tropical and subtropical regions of the Gulf of Mexico, and especially in monsoon-type areas where *estuarinization* of the continental shelf occurs (i.e., in front of Tampa Bay, Apalachicola Bay, and along the coasts of Mississippi, Louisiana, Texas, Veracruz, Tabasco, and Campeche), the difference between lagoon-estuarine areas and the inner shelf is smaller than in areas where the monsoon-type winds are unimportant. There are also sufficient descriptions of specialized estuarine fish faunas for it to be clear that they exist in the Gulf of Mexico, where the size of the estuaries and their tidal regime permit a relatively long flushing period (Gunter, 1957, 1967). If the Guntherian hypothesis of estuarine dependence of continental shelf, fish stocks cannot be applied for the tropical regions as a whole (Longhurst and Pauly, 1987), at least it can be applied in a straightforward manner to the tropical and subtropical regions of the Gulf of Mexico, especially the soft-bottom communities of the inner shelf associated with extensive deltaic systems, significant river discharge, and broad areas of coastal vegetation

(Deegan et al., 1986; Pauly, 1986b, 1998; Pauly and Yáñez-Arancibia, 1994; Baltz et al., 1993, 1998; Chesney et al., 2000, Chesney and Baltz, 2001; Sánchez-Gil and Yáñez-Arancibia, 1997; Sánchez-Gil et al., 2008; Yáñez-Arancibia et al., 1993, 1988, 1998, 2007).

A significant fraction of the harvested secondary production in the western Gulf's ''fertile crescent'' (Mississippi River mouth to the northern tip of the Yucatan Peninsula, and including some areas the Atlantic coast of Central America) is derived from estuarine ecosystems, including areas on the shallow shelf influenced by estuarine plumes (Darnell, 1990; Chesney and Baltz, 2001; Yáñez-Arancibia, 2005; Sanchez-Gil and Yáñez-Arancibia, 1997; Sanchez-Gil et al, 2008). Characteristics of these estuaries are high riverine discharge rates, large fresh water surpluses, and low water residence times. Much of the production and subsequent trophic transfer may therefore occur outside the physical boundaries of the estuaries, that is, in association with plumes of fresh water over the inner continental shelves. These contrasting sources—estuary and shelf—of trophic delivery to the fishery forage base, and ultimately to larger consumers, is one cause of uncertainty on how we view the functions of estuaries and the shelf ecosystem they influence.

Thus, high fisheries production may be attributable in part to the lagoon- and estuary-like conditions prevailing in large parts of the inner continental shelf during high river discharge periods, as relatively a few fish species are wholly adapted to life cycles within lagoon-estuarine systems. Moreover, in the subtropical and tropical parts of the Gulf, and especially in areas where high river discharges lead to the shelf exhibiting estuary-like conditions, the distinction between estuaries and the shallow shelf is clearly smaller than in other areas (Longhurst and Pauly, 1987; Pauly and Yáñez-Arancibia, 1994; Yáñez-Arancibia et al., 1994; Yáñez-Arancibia, 2005).

As a consequence, if the ''recruits'' (= young fish) utilize estuaries and coastal lagoons, the population in question will be ''estuarine dependent.'' If the recruits to that population regularly utilize the estuarine plume on the inner continental shelf, then they will be ''estuarine-related,'' or simply opportunistic. For estuarine-dependent species, seasonal and interannual variation in environmental conditions (e.g., temperature and salinity) may serve as ecological filters that define the quantity of suitable habitat for early life history stages. Utilization of coastal habitat types, particularly with regard to estuarine dependence, the occurrence of a life history stage in more than one habitat type is insufficient to refute the hypothesis of nursery function of a given habitat

type. A species may be estuarine dependent at one end of its range and less so at the other end. It is the controlling variables that are important, not the biologist's definition and characterization of a habitat type.

Nevertheless, Yáñez-Arancibia (2005); Cowan et al. (2008); Baltz and Yáñez-Arancibia (2010) preferred to take a fish's eye view of the habitat and used the distribution and abundance of a species or life history stage, rather than environmental gradients, to define its habitat. Using this approach, a species may be characterized as estuarine dependent if one of its life history stages requires some combination of environmental conditions typically found in estuaries. Environmental conditions that control recruitment success for a species may vary across its range, such that a species may be dependent on estuaries at locations throughout most of its range, but rely heavily on sea-grasses-covered coastal sand flats at another location. The identification of nursery habitat types should require at least a comparison of the densities of early life history stages in other nearby habitat types, but a better characterization would derive from identifying where enhanced survival, growth, and recruitment occur.

18.5.3 Habitat Protection As a Management Tool

A number of investigations have demonstrated the existence of complex, seasonally changing relationships between fisheries yields and high nutrient loads, fresh water inputs, shallow depths, large areas of tidal mixing, coastal vegetated area, surface area of lagoon-estuarine systems, and the resulting high productivities that are typical of estuaries and estuarine plume ecosystems (Deegan et al., 1986; Nixon, 1988; Iverson, 1990; Sanchez-Gil and Yañez-Arancibia, 1997; Yáñez-Arancibia et al., 2007; see figures in Day et al., 1989). As a result of these relationships, and despite the small aggregate spatial extent of estuaries (< 1% of the global marine area), a fraction exceeding 50% of US and Mexico fishery yields have historically been derived from estuarine or estuary-dependent species (Gunter, 1967; McHugh, 1967; Houde and Rutherford, 1993; Vidal-Hernandez and Pauly, 2004).

Thus, management decisions must account for this seasonal pulsing habitat, and the protection of its different components, including the aquatic vegetation, in the context of comprehensive environmental planning. Coastal fisheries resources are an expression of ecosystem functioning and to assure the persistence of such resources, the protection, and conservation of essential habitats is the key.

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CHAPTER NINETEEN

HUMAN IMPACT AND MANAGEMENT OF COASTAL AND ESTUARINE ECOSYSTEMS

John W. Day Jr., Alejandro Yáñez-Arancibia, and W. Michael Kemp

Humans have lived near and prospered from estuaries for tens of thousands of years. Many ''cradles of civilizations'' were located near estuaries of the Tigris–Euphrates, Nile, Indus, Usumacinta, and Yellow rivers (Day et al., 2007, 2012). Initially, the abundance of food invited human settlements. Later, river mouths became important sites for commerce, and at present, many of the world's largest cities border major estuarine systems, including New York, London, Cairo, Calcutta, Dacca, Sao Paulo, Buenos Aires, Guayaquil, and Shanghai. From the beginning, human activities resulted in alterations in the natural state of estuaries. Early examples include construction of mounds for home sites and harvesting of fish and shellfish. Human impacts have continued through the centuries, so that at present, there are almost no estuarine systems in their natural state. The rate and degree of human impact have accelerated over the past two centuries as a result of increasing population, industrial growth, and the development of new technologies such as modern dredges and powerful pumps. As the effects of different kinds of impacts can build slowly over time and can be synergistic, W. E. Odum (1970) called the effects of human activity the ''insidious alteration of the estuarine environment.''

In a synthesis of coastal ecological systems of the United States, Odum et al. (1974) discuss the effects of a number of specific types of impacts from the perspective of new energy inputs altering older natural energy flows.

In this chapter, we discuss specific ways that human activities affect estuarine ecosystems. Over the past several decades, there has been a great deal of scientific study of human impacts on estuaries. A complete review of this literature would take considerably more space than this entire volume. In this chapter, therefore, we want to do only a few things. First, we present a generic classification scheme that organizes impacts into a few major types. We then give examples of each type of impact for a number of different estuarine systems based on information presented earlier in the book. In doing so we accomplish two things: we demonstrate the responses to different kinds of impacts and we show how human impacts affect different aspects of the structure and function of estuarine ecosystems such as primary production, nutrient cycling, and community structure. Finally, we discuss an integrated approach to coastal management. A number of texts have dealt with various aspects of human impacts in coastal

TABLE 19.1 Classification of human impacts on coastal ecosystems

Impact Type	Examples
Physical changes	
Hydrologic changes	Channelization of streams, canals for petroleum production in Mississippi delta, oil exploration, dredging, drainage, harbor dredging, and navigation
Impoundments	
Reclamation	Polders in the Netherlands
Enrichment	
Eutrophication	Algal blooms resulting from agricultural runoff
Organic enrichment	Fish-processing wastes
Thermal additions	Power plants
Toxins	Heavy metals, pesticides, other chemicals such as DDT and PCBs, mercury, exotic organics
Direct changes in species	
Composition	Harvest and overharvest, overfishing
Introduction of exotic species	Striped bass on US west coast, nutria in Louisiana

systems, and the reader may want to consult these for more detailed treatments (Olsen and Burgess, 1967; Odum et al., 1974; Gerlach, 1981; Neilson and Cronin, 1981; McLusky and Elliott, 2004; Kennish, 2005; Orth et al., 2006; Withers and Nipper, 2007; Costanza, 1994; Fanning et al., 2011; Yáñez-Arancibia and Day, 2012).

19.1 A CLASSIFICATION OF HUMAN IMPACTS IN ESTUARIES

We identify four general categories of impacts on estuarine ecosystems: enrichment with excessive levels of organic material, inorganic nutrients, or heat; physical alterations; introduction of toxic materials; and direct changes in community structure through the harvesting or introduction of exotic species (Baltz and Yáñez-Arancibia, 2012). Table 19.1 outlines this classification and gives examples of each type of impact.

Enrichment is the addition of generally naturally occurring substances or heat at levels that are not toxic but that lead to changes in the structure and metabolism of the ecosystem. Eutrophication is a type of enrichment that occurs as a result of the addition of high levels of inorganic nutrients, especially nitrogen and phosphorus. The addition of excess heat is generally called thermal pollution or calefaction. *Physical alterations* are direct changes in the physical structure or dynamics of an estuary. Physical alterations are mainly of two related types: hydrologic changes and reclamation. In this chapter, we define hydrologic changes as those that alter water movement but not to the extent that the system is completely destroyed (e.g., the system retains a wetland or estuarine character). Reclamation is the conversion of an estuarine system to dry land by drainage and/or filling. As it implies, the introduction of *toxic materials* is the introduction of materials that are toxic to organisms, either acutely or chronically. Toxins can be naturally occurring materials such as heavy metals (which occur in concentrations much higher than that which occurs naturally) or exotic organic compounds such as pesticides or by-products of industrial activity. *Excessive fisheries harvest or introduction of exotic species* leads to direct changes in species composition. These usually lead to changes in the relative abundance of different species, but if harvest pressure is great enough for a sustained period, species may be driven to extinction in a local area. In the remaining sections of the chapter, each of these types of impacts is discussed in more detail and several examples of each are given to illustrate the kinds of changes that can occur. Specific examples of human impacts are given in many chapters in this book, and we refer to these in this chapter.

19.2 ENRICHMENT

Progressive enrichment of estuarine waters with inorganic nutrients, organic matter, or heat leads to changes in the structure and processes of estuarine ecosystems.

19.2.1 Nutrient Enrichment and Eutrophication

Nutrient enrichment can lead to excessive algal growth, increased metabolism, and changes in community structure, a condition known as *eutrophication*. There have been many studies of eutrophication in coastal waters (Neilson and Cronin 1981, Nixon 1995, Cloern 2001, Kemp et al. 2005, Withers and Nippers 2007). Jaworski (1981) discusses the sources of nutrients and the scale of eutrophication problems in estuaries. The following examples discussed further serve to illustrate the effects of excessive nutrient enrichment in estuaries. In Chapters 4 and 5, the impact of overenrichment with nutrients is

discussed for phytoplankton and submerged aquatic vegetation.

With progressive nutrient enrichment, phytoplankton form dense "blooms" that can discolor affected waters and cause water quality problems (Paerl, 1988; Richardson, 1997; Anderson et al., 2000). When blooms die, they sink to the seafloor and decompose, causing oxygen depletion in bottom waters (i.e., hypoxia and anoxia) (Officer et al., 1984; Rabalais and Turner, 2001; Diaz and Rosenberg, 2008). Some bloom species also produce foul odors and tastes, which can be problematic from water supply, recreational, and aquaculture perspectives. Some species also produce secondary metabolites that can be toxic to higher fauna (Carmichael, 2001), including zooplankton, fish, and a variety of mammals, including humans. Details on these impacts are presented in Chapter 4.

Deterioration of seagrass and related submersed plant beds has been observed over wide geographical scales (e.g., Duarte, 2002; Waycott et al., 2009), and it has been estimated that nearly 30% of worldwide submersed plant area has been lost since the 1870s and that the rate of loss continues to increase (Chapter 5). A complex network of interactions exists between submersed plants, hydrodynamics, sediment, and associated organisms, which can result in positive feedback effects on plant growth (Chapter 5). Submersed plant communities include the vascular plants themselves and a complex epiphytic community that grows on the plant leaves. Because of this, submersed plants are very sensitive to reductions in light. In effect, there is a double light filter before radiation can drive plant photosynthesis. Light has to pass through the water column and then through the epiphytic community before reaching the leaf surfaces. In a clean environment, there is a dynamic balance of light, nutrients, submersed plants, and the epiphytic community. However, eutrophication can destabilize this balance. When there is point and nonpoint source runoff into an estuarine system, water column transparency can be reduced due to both suspended material in the runoff and nutrient-stimulated phytoplankton growth. In addition, excess nutrients result in overgrowth of the epiphytic community. Because of these processes, submersed plants are acutely sensitive to eutrophication and, as indicated earlier, large areas of SAV have disappeared (Kemp et al. 2004).

19.2.2 Addition of Excessive Levels of Organic Matter

The enrichment of coastal waters with excessive levels of organic matter is caused by inputs of material from a variety of different sources and leads to a number of changes. The source of high levels of organic matter can be sewage waste water as well as seafood processing wastes and industrial effluents. These wastes lead to bacterial contamination and lowered dissolved oxygen concentrations and can result in very large changes to community structure and metabolism. Inorganic nutrients from mineralization of the organic matter can stimulate dense algal blooms and maintain excessive levels of organic matter. Therefore, the impacts of excessive nutrients and organic matter are often similar.

When an area is enriched with organic matter, the structure of the benthic community can change dramatically. Organisms that burrow into anaerobic sediments have to be able to oxygenate their burrows by pumping oxygenated water through. With increasing organic loading of an area, from sewage pollution, for example, burrowing organisms are eliminated because the anaerobic zone moves closer to the sediment surface. In grossly polluted areas, only worms such as *Capitella* sp. can survive, and they may do very well by consuming organic matter at the sediment surface (Mann, 1982).

In the Scheldt Estuary in Belgium, high loading of organic matter from wastewater treatments plants (Soetaert et al., 2006) and watershed runoff have led to high bacterial respiration, and the estuary has become net heterotrophic in spite of high phytoplankton production (Gazeau et al., 2005; Kromkamp and Van Engeland, 2010, see Chapter 15 for more details).

19.2.3 Thermal Additions

One of the most commonly described impacts of power generation is often referred to as *thermal pollution*, although calefaction or thermal loading may be more appropriate (Hall et al., 1978). Under certain conditions, heated water from power generation facilities such as coal burning and nuclear power plants can selectively eliminate large segments of a healthy aquatic ecosystem; however, most often, the impacts are less pronounced. Impacts on individuals include interference with physiological processes, behavioral changes, enhancement of disease, and impacts from changing gas solubilities. In temperate winter, fishes may become thermally marooned in the warm water around power plants, with seasonal decline in ambient temperature.

19.3 PHYSICAL ALTERATIONS

19.3.1 Local Alterations

Physical alterations within coastal systems include activities such as filling and draining of wetlands,

construction of deep navigation channels through shallow water bodies, bulkheading, and canal dredging through wetlands. Two major types of impacts resulting from these activities are habitat destruction and hydrologic or hydrodynamic alteration. For example, canals and deep navigation channels can alter circulation, allow saltwater intrusion, and promote the development of anoxic waters in the bottoms of channels.

One of the major physical alterations of coastal systems is the direct destruction of wetlands. A number of both natural and cultural factors lead to wetland loss (Table 19.2), but in general, cultural factors are much more important. Wetlands along the US coast in areas with high population densities have generally suffered the greatest proportional loss (Gosselink and Baumann, 1980), a reflection of the pressure of development in these areas.

TABLE 19.2 Activities and processes causing wetland loss

Impact Type	Examples
Cultural	Direct
	Dredging
	Spoil disposal
	Land fill
	Waste disposal
	Impounding and draining (e.g., for agriculture)
	Marsh buggies and other wetland transportation vehicles
	Indirect
	Sediment diversion (e.g., dams, deep channels), hydrologic alterations (e.g., by canals, spoil banks)
	Subsidence due to extraction of groundwater, oil, gas, sulfur, and other minerals
Natural	Subsidence (apparent water level rise)
	Isostatic adjustments (e.g., crustal downwarping or uplift)
	Differential consolidation of sediments because of textural variability
	Consolidation of sediments because of weight of other features (e.g., natural or artificial levees, buildings)
	Eustasy
	Droughts
	Hurricanes and other storms
	Erosion
	Biotic effects (e.g., muskrat and goose eat-outs)

Source: From Gosselink and Baumann (1980).

The deltas of the Mississippi and Ebro rivers serve as two examples where human activities have resulted in dramatic regional changes in coastal systems (Chapter 6). In the Ebro delta, changes have proceeded deliberately to provide freshwater supply and land for urban development and agriculture. In the Mississippi delta, many of the changes have followed as the indirect and cumulative impacts of human activities such as levees, pervasive hydrological alteration, and petroleum exploration and production. In both cases, large areas of coastal ecosystems have been altered and destroyed. Such human alteration of deltaic ecosystems is pervasive worldwide (Syvitski et al., 2009; Vörösmarty et al., 2009; Day et al., 2011)

19.3.2 Upstream Alterations

Upstream changes in rivers can have pronounced effects on the estuaries into which they discharge. Construction of dams, diversion of fresh water, and groundwater withdrawals lower the amount of fresh water, nutrients, and suspended sediment input. We have documented in a number of chapters in this book the importance of these inputs to estuarine productivity (Chapters 2, 4, 6, 13, and 18). Dams also impede or block the movement of migratory organisms, and by changing the timing of water discharge, they may interfere with the life histories of migratory fish that are finely tuned to those discharges. On the other hand, channelization of streams causes more rapid pulses of water to coastal systems. Construction of dams on the Mississippi River system has resulted in about a 50% decrease in suspended load, undoubtedly aggravating the land loss problem in the Mississippi delta while these sediments fill up the upstream reservoirs. Blum and Roberts (2009) projected that almost all delta wetlands would disappear by the end of this century because of sediment reduction and sea-level rise. Freshwater diversions from the Colorado River in the western United States are causing hypersaline conditions and deterioration of the river delta. Because most of the water use occurs in the United States but the coastal problems are felt in Mexico, this issue has been an important point of contention and discussion between the two countries. Freshwater and sediment reductions in rivers have impacted coastal systems fed by many rivers including the Ebro in Spain, the Euphrates, the Nile, and the Indus rivers (Syvitski et al., 2009). Stanley (1988) reported that the eastern part of the Nile delta was undergoing subsidence of about 0.5 cm/year. This rapid subsidence combined with reduction of sediment input due to the Aswan Dam and rising sea level is likely to lead to flooding of a large part of the delta plain by the end of the next century.

19.4 TOXINS

Toxic materials include compounds such as pesticides, heavy metals, petroleum products, and exotic by-products of industrial activity. These materials can be acutely toxic, or more commonly, they can cause chronic or sublethal effects. Human-introduced chemical contaminants bind to sediments in estuaries, and some, including methyl mercury, selenium, PCBs, and trace metals, bioaccumulate up the estuarine food chain (Takekawa et al., 2006).

The toxicology literature is filled with data reporting ecosystem metabolic responses to diverse organic and inorganic contaminants (Graney et al., 1994; Chapter 15). For example, Wiegner et al. (2003) reported that ecosystem production was significantly stimulated by nutrients and inhibited by metal toxins, while input of both sets of chemicals resulted in slight enhancement of gross and net production. Herbicide additions to seagrass-dominated mesocosms resulted in sharp declines in production that diminished within weeks as the herbicides degraded (Cunningham et al., 1984). In Chapter 11, Benfield reports on both acute and lethal impacts of toxins on zooplankton. Many estuarine sediments serve as long-term sinks for a variety of classes of toxic chemicals, including heavy metals, hydrocarbons, herbicides, pesticides, and endocrine disrupters, and thus, benthic organisms can be subjected to more toxic stress than organisms in the water column (Long, 2000, see Chapter 12). Generally, studies have shown that crustaceans and echinoderms are intolerant to most kinds of sediment contamination and small-bodied deposit feeders, that is, annelids and nematodes, are the most tolerant. As a result, pollution may bring about community change due to indirect effects, in which tolerant species change in abundance because competitors, predators, or prey are affected by pollutants (Fleeger et al., 2003). Because wildlife species are often at the top of the food chain, they can be strongly impacted by toxins (Chapter 14). For example, PCB contamination in coastal Georgia marshes was found to be associated with a high frequency of strand breakage in the DNA of clapper rails (Novak et al., 2006). This level of contamination has human health ramifications because the rails are game species commonly hunted and consumed by local residents. Mercury contamination can be a particularly severe problem (Takekawa et al., 2006), causing acute toxicity in birds and mammals. High-level exposure damages the central nervous system, while low-level exposure affects reproduction in vertebrates (Wolfe et al., 1998).

The environmental impacts of petroleum extraction, processing, and transport in the coastal zone have been a concern for many years. This is especially true for areas with high levels of petroleum activity such as the Mississippi delta or the Usumacinta/Grijalva delta (Withers and Nipper, 2007). Ko and Day (2004) reviewed the literature on the environmental impacts of petroleum activities in the delta. These included mortality, growth inhibition, reduced reproduction, shifts in species importance, and tainted flesh in fish and shellfish. Teal and Howarth (1984) stated the following generalizations: ''oil regularly reaches sediments after a spill; oil in anoxic sediments is persistent; oil regularly contaminates zooplankton and benthic ínvertebrates; fish are also contaminated, but to a lesser extent; and oil contamination decreases the abundance and diversity of benthic communities.''

One phenomenon that often characterizes persistent toxins is the biological concentration of a substance as it moves up through a food web. This process has been called *bioaccumulation* or *biomagnification*. There are many examples of this for persistent pesticides. One classic example is for DDT in a salt marsh system on the shore of Long Island Sound, New York. Woodwell et al. (1967) measured the concentration of DDT and several breakdown products in the water, soil, and biota of the estuary. DDT concentrations increased with trophic level by more than 5 orders of magnitude. Concentrations ranged from 0.00005 ppm in water to 75.5 ppm in ring-billed gulls. The highest concentrations were close to being acutely toxic. Bans on the use of such persistent pesticides in many parts of the world have decreased the incidence of the problem, but this example vividly illustrates the process of biomagnification.

19.5 CHANGES IN BIOTIC STRUCTURE DUE TO HARVEST AND INTRODUCTION OF NEW SPECIES

19.5.1 Harvest

One of the attractions of estuaries is that they often support a high fisheries production (Baltz and Yáñez-Arancibia, 2012). If an individual species is exploited too heavily or is overfished, there can be pronounced changes in the composition of the estuarine community (Houde and Rutherford, 1993; Wilson, 2002; Musick et al., 2000). Houde and Rutherford (1993) reported that some estuarine-dependent

fisheries have declined, probably due to overfishing. Wilson (2002) reported that many estuarine fisheries are being overexploited, with several species highly endangered, including smelt, eels, oysters, and sturgeons. In Chapter 18, there are a number of additional examples of the effects of depletion of the stocks of individual species.

One kind of industrial activity in the coastal zone that can be considered as a kind of accidental harvest is the trapping of fish and plankton in the cooling water intake of power plants and other facilities. This has been termed *entrainment* and can lead to significant mortality because of the enormous amounts of water that can pass through a plant. Because the majority of the estuarine fauna have planktonic larvae and many important fishery species are both estuarine dependent and have planktonic life stages, entrainment holds enormous potential for both ecological as well as economic damage.

19.5.2 Introduction of New Species

The introduction of new species into coastal ecosystems has taken place for many centuries, both on purpose and by accident. Purposeful introductions have mainly been commercially or recreationally valuable fish and shellfish, although some species have been introduced for utilitarian reasons such as weed control. Most accidental introductions of new species into coastal and estuarine waters have been on the hulls or in the ballast water of ships. Some species were purposely imported and then accidently released. Below, we discuss each of these in more detail.

Moyle (1986) reviewed fish introductions into North America. The transplantation of fishes has a long history. The Romans took carp from the Danube River to Italy, and the Scandinavians transplanted salmonids in the twelfth century. By the 1870s, Pacific salmon were regularly brought to the Atlantic coast. The introduction of new species, not only of fish but also of other aquatic organisms continues to the present.

One introduced species that has become important in coastal areas around the Gulf of Mexico is the nutria (*Myocastor coypu*). The nutria, a native South American mammal, was introduced into Louisiana in the 1930s for fur production and weed control (O'Neil, 1949; Lowery, 1974). Subsequently, the nutria spread rapidly and its population grew, and by the late 1950s, the total population was estimated at over 20 million animals (Lowery, 1974). It is now the single most important species in the trapping industry in Louisiana. Nutria may also be contributing to the coastal wetland loss problem in Louisiana. Because they cause extensive "eat-outs" of existing marsh and feed heavily on new shoots, they contribute to marsh destruction and regrowth (Evers et al., 1998; Visser et al., 1999). It has become apparent that nutria are an important factor preventing the regrowth of cypress forests because they feed heavily on seedlings (Conner, 1988; Shaffer et al., 2009; Myers et al., 1995). The nutria is thus a case where a single species can be both beneficial (in terms of the fur harvest) and detrimental (contributing to wetland loss).

19.6 COASTAL AND ESTUARINE MANAGEMENT IN THE TWENTY-FIRST CENTURY

Over much of the past several decades, solutions to environmental impacts as discussed earlier in this chapter, and throughout this book, have often been addressed individually. If a sewage plant or industry was polluting an estuary, the goal was to use more advanced sewage treatment or remove toxins from the industrial effluent. In the twenty-first century, the goal of management is moving toward integrated coastal zone management (ICZM) that deals holistically with coastal problems while taking into account megatrends of this century such as climate change and energy scarcity (Day et al., 2009; Withers and Nipper, 2007; Fanning et al., 2011; Yáñez-Arancibia et al., 2011, 2012). In the following section, we describe the approach of ICZM.

19.6.1 Integrated Coastal Zone Management (ICZM)

ICZM is a multidisciplinary, multisectoral dynamic process, by which the decisions on use, development, and protection of coastal areas and their natural resources imply a balance among land use, climate, and landscape, with the potential for land use change in parts of the coastal zone and protection of certain natural areas, and it should be done in a way that balances ecological, social, and economic factors. ICZM is science based and addresses a host of interrelated environmental problems (Harwell et al., 1999; Mitsch et al., 2001; Day et al., 2005; Harwell et al., 1996; Twilley et al., 1998; Gentile et al., 2001; Reyes et al., 2004; Ko and Day, 2004; Yáñez-Arancibia et al., 2011) and integrates multiple system components and uses. ICZM helps identify and strives for sustainable outcomes, avoids deleterious actions, and achieves adaptive management (Boesch, 2006; Yáñez-Arancibia and Day, 2012). ICZM integrates all

levels of governments, NGOs, and communities in a program for the protection, conservation, and sustainable development of coastal environments and resources. (Yáñez-Arancibia, 2004; Hinrichsen, 2011).

Ecological risk assessment is an integral component of ICZM (Christensen et al., 1996; Harwell et al., 1996; Gentile et al., 2001; Boesch, 2006; Day and Yáñez-Arancibia, 2012). Decision making is facilitated by characterizing the ecological risk or consequences of alternative policies in the context of sustainability goals. The successful implementation of ICZM is based, in part, on using a risk-based process to identify the causal linkages among land uses, stressors, and ecological effects in order to base management decisions on sound science and specific societal goals for ecological restoration.

From the standpoint of temporal and spatial scales, ICZM integrates across the continuum from the river basin, the estuarine ecosystem to the estuarine plume on the continental shelf and from seasonal to decades or longer (Fig. 19.1). The goals of ICZM are to reduce those market distortions that affect biological diversity, align incentives to promote biodiversity conservation and sustainable use, and internalize costs and benefits in the ecosystem to the extent feasible. ICZM recognizes that management based on ecosystem integrity and functioning is most likely to be sustainable. In addition, ICZM must contend with a shifting baseline because of global climate change and growing energy scarcity.

19.6.2 Global Climatic Change and Energy Scarcity

In Chapter 20, the impacts of climate change are discussed. Because of the location of coastal systems at the boundary between the land and the sea, they are among the most threatened by climate change. Global change impacts on coastal systems include increasing temperature; changes in precipitation, frequency of drought, and fresh water input; salinity intrusion; accelerated sea-level rise; ocean acidification (Waldbusser et al. 2011) and increase in strong storm frequency and strength. Climate change induces uncertainties in the environmental stability of critical coastal habitats and their economic development. Current and future ICZM must take climate change into consideration as one of the most important forces impacting coastal systems (Day and Templet, 1989; Twilley et al., 2001; Scavia et al., 2002; Day et al., 2005, 2008, 2012; Poff et al., 2002; Ning et al., 2003; Viles and Goudie, 2003).

There is increasing evidence that world conventional oil production has already peaked and that total oil production (all-liquids) will peak within a decade (Fig. 19.2), implying that demand will consistently exceed supply and that energy cost will increase significantly (Campbell and Laherrere, 1998; Deffeyes, 2001–2010; Hall et al., 2003; Hall and Day, 2009; Heinberg, 2003; Association for the Study of Peak Oil, 2008). Global production increased exponentially until about 1970, but the rate of increase has declined since. Production is now three to four
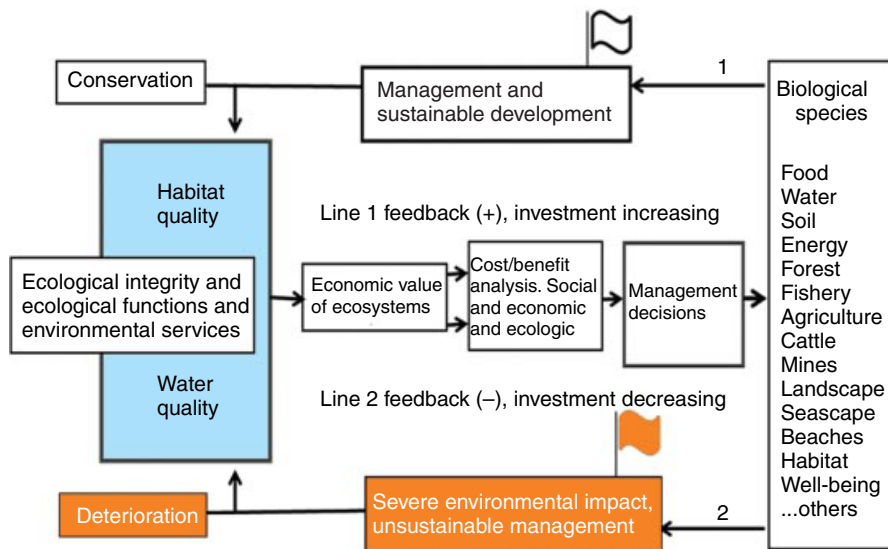
FIGURE 19.1 Environmental sustainability and the economic development of the coastal zone, indicating the importance of ecosystem feedback to sustainability, the economic value of ecosystems and resources, support for management decisions, and sustainable development perspective as a function of ecological integrity measures such as habitat quality, water quality, biodiversity, and ecological functions. *Source*: Modified from Yáñez-Arancibia et al. (2009a).
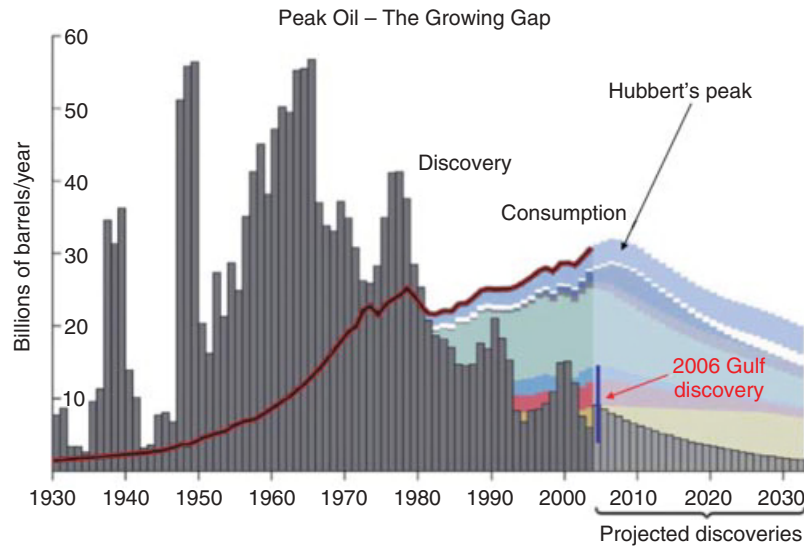
FIGURE 19.2 Worldwide oil discovery and consumption from 1930 until the present, and projected future discoveries. Most of the major discoveries were made before 1980. The present world consumption is four to five barrels for each barrel discovered, with most of the production coming from fields discovered three to four decades ago. *Source*: Printed with permission from the Association for the Study of Peak Oil (ASPO 2008).

times the discovery rate, and current production is mostly from giant and supergiant fields discovered 30–40 years before 1960 (Skrebowski, 2004). Of these, roughly a quarter are declining in production at an average rate of about 4% annually. Also, world oil demand is increasing, especially in China and India.

An important factor that affects consideration of energy use is the net yield of energy in a production process, or of the energy return on investment (EROI). EROI of conventional world oil production was as high as 100 : 1, but over the intervening decades, it fell to between 15 : 1 and 10 : 1 for producing fields (Cleveland et al., 1984; Hall et al., 1986; Hall and Day, 2009; Murphy and Hall, 2011). Thus, it is costing more energetically to find and produce oil. The EROI for nonconventional sources of oil (oil shale and oil sands) and most renewable energy sources are all less than 15 : 1, and most are far less than 10 : 1 (Heinberg, 2003; Hall and Day, 2009; Bardi, 2011). The implication for coastal management, and for all natural resource management, is that energy intensive management approaches will become increasingly unaffordable (Day et al., 2005, 2009). Thus, as climate change makes management increasingly more challenging, energy scarcity will make it more expensive and limit options.

19.6.3 Ecological Engineering and Ecological Economics

In a time of energy scarcity, we suggest that ecotechnology, and more specifically ecological engineering, are appropriate bases for sustainable coastal management. Ecological engineering is the design of sustainable ecosystems that integrate human society with the natural environment for the benefit of both (Mitsch and Jørgensen, 2004). Because it uses mainly natural energies, it is very energy efficient. The primary tools are self-designing ecosystems with the components mostly biological species and processes. Ecological engineering is different from environmental engineering that includes things such as conventional sewage treatment. The goals of ecological engineering are (i) the restoration of ecosystems that have been substantially disturbed by humans, (ii) the development of new sustainable ecosystems that have both human and ecological value, and (iii) the maximization of use of natural energy and reduction of fossil energy consumption.

Self-design and (the related concept) self-organization are important properties of created and restored ecosystems (Mitsch and Jørgensen, 2004). Self-organization is the property of systems to reorganize themselves in environments that are inherently unstable and nonhomogeneous. Organization is not derived from outside forces but from within the system. Self-design is important in times of scarcity, because ecologically engineered ecosystems tend to take care of themselves and are less energy demanding. Self-organization develops flexible networks with a much higher potential for adaptation. Implicit in ecological engineering and self-design is the fact that the functioning of the natural systems should form the basis for sustainable

management; working with nature rather than against it is inherently more energy efficient.

19.6.4 System Functioning as a Basis for Sustainable Management

Throughout this book, various authors have emphasized the variability of estuarine systems, and this variability is central to the functioning of these systems. A key concept of ICZM is that sustainable management will be most successful when it is based on ecosystem functioning (Day et al., 1997; Yáñez-Arancibia et al., 2011, 2012; Yáñez-Arancibia and Day, 2012). This means that management activities should integrate ecosystem functioning and, insofar as possible, allow the system to self-design and self-regulate naturally (Day et al., 1997; Mitsch and Jørgensen, 2004). Two important concepts that are especially pertinent to lower river floodplains and coastal areas are the flood pulse concept for lower rivers and their flood plains (Junk, 1999; Junk et al., 1989) and the pulsing concept for coastal systems, as exemplified for the Mississippi river basin and delta (Day et al., 1997), Apalachicola Bay (Livingston, 2000), and the land–ocean interactions in the Mexican Gulf coast (Yáñez-Arancibia et al., 2004, 2007).

The flood pulse concept considers the importance of hydrology and hydrochemistry of the river itself but focuses on the exchange of water, nutrients, and organisms between the river and the connected floodplain (Junk et al., 1989; Junk, 1999). Periodic inundation is the driving force in a river–floodplain ecosystem. The pulsing concept states that coastal systems and deltas are structured and sustained by a hierarchical series of overlapping energetic forcing or pulsing events that vary on spatial and temporal scales. Ecologists, climatologists, and geomorphologists have identified a range of different modes of pulsing, which seem to be essential components of the behavior of coastal systems. These events range from switching of river channels in deltas that takes place on the order of 500–1000 years to daily tides and includes great floods that occur a few times a century, strong storms such as hurricanes occurring on decadal scales, annual river floods, and frontal passages (Day et al., 1995, 1997, 2003; Viles and Goudie, 2003; Yáñez-Arancibia et al., 2004, 2007).

19.6.5 Environmental Sustainability and Socioeconomic Development

The success of sustainable economic development of the coastal zone depends on a balanced approach for development that does not compromise the integrity of the coastal marine environment. Elements for this approach must include avoiding ecological deterioration, characterizing sustainable development, quantifying ecological and environmental damage, developing and refining methods to determine environmental quality, quantifying ecological functions, and economic valuation of natural resources (Yáñez-Arancibia et al., 2009). Another important criterion to consider is the intrinsic economic value of coastal resources. These resources represent a "natural capital" that supports the economic health of the society. The goods and services provided by the natural capital represent the "interest" generated by human investment in natural ecosystems (Costanza et al., 1997; Yáñez-Arancibia, 1999). These values can be enormous. For example, Batker et al. (2010) reported that the value of ecosystem services for the Mississippi delta ranged from $12 billion to $47 billion annually with a natural capital asset value of $330 billion to $1.4 trillion. Environmental sustainability and the economic development of the coastal zone are closely related with the economic value of ecosystems and resources; this is key to support management decisions (Fig. 19.1). The sustainable development perspective as a function so ecological integrity requires that measures such as habitat quality, water quality, biodiversity, natural production mechanisms, and ecological functions need to be integrated in any conceptual model toward integrating healthy ecology with a healthy economy (Yáñez-Arancibia et al., 2009). Social and economic development pressure in many coastal areas may be reaching a threshold where there could be a dramatic crisis in environmental sustainability in the near future.

19.7 CONCLUSIONS

In the chapter, we have discussed impacts individually so as to indicate clearly their causes and consequences. It should be clear at this point that there are serious problems in many, if not most, coastal systems. These problems are almost always due to multiple stresses. The ecological damage in many systems is staggering, and if steps are not taken, more ecological resources with considerable economic value will be lost. To effectively address these multiple stresses, an integrated approach is needed. The ICZM is such an approach. We finish this chapter with a few examples of coastal systems with multiple stresses.

Nichols et al. (1986) provide an excellent summary of changes in the San Francisco Bay estuary.

Extensive hydraulic mining in the drainage basin in the second half of past century greatly altered streams feeding into the bay system and deposited considerable sediments in the bay. Of the original 2200 km^2 of tidal marsh, only about 125 km^2 of undiked marsh remains at present. Owing to extensive use of freshwater for irrigation and domestic consumption, fresh water inflow to the bay system has been reduced by about 60%. This disruption of flow has affected migratory fish populations. Considerable numbers of young fish are drawn into irrigation pumps and siphons, and the abundance of striped bass, for example, has declined to 25% of that of the mid-1960s. Wastes from industry, municipalities, and agriculture flow into the bay and historical fishery levels have declined. Management of this system includes dealing with toxins, restoring freshwater inflows, and creating or restoring wetlands.

Data presented for the Mississippi Delta, the Chesapeake Bay, and the Ebro delta show similar impacts. In these areas, there have been large reductions in habitat, widespread eutrophication, pollution by toxic materials, and decreases in fisheries. For example, large areas of coastal wetlands in these three areas have been lost and there have been significant reductions of submerged aquatic vegetation in the Chesapeake Bay. Unfortunately, this picture of pervasive alteration of the estuarine environment is all too common around the world. Although there is much concern and activity, the situation may not be improving much, and in the developing world, the pace of degradation seems to be accelerating. In the developing world, however, environmental protection is viewed as a luxury, even though many more people there depend on estuaries for their direct economic well-being. Globally estuaries are preferred sites for human habitation, and hence are very heavily impacted. There is as yet no general plan for alleviating these problems and conserving these important resources. There is much for the readers of this book to do.

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GLOBAL CLIMATE CHANGE AND ESTUARINE SYSTEMS

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It is interesting to note that practically all of the estuaries discussed in this book did not exist 10,000–15,000 years ago and that they will cease to exist in the near geologic future. The world's present estuaries were formed when sea level rose after the last glaciation

(Day et al., 1989)

20.1 INTRODUCTION

It is ironic that the very process that led to the formation of modern estuaries, sea level rise (SLR), may now contribute to their rapid demise. Indeed of all of the manifestations of climate change and global warming, none have captured the imagination as much as the specter of increasing rates of SLR. Perhaps this is because we have already witnessed the effects that high rates of relative SLR (SLR + land subsidence) have had on coastal cities such as Venice, Italy and New Orleans, Louisiana. Or perhaps it is just that it is easier for us to imagine the dramatic effects of coastal flooding on human infrastructure as opposed to the more subtle, but no less troubling effects of increased atmospheric carbon dioxide on ocean acidification or reductions in freshwater input on estuarine productivity, for example. SLR, however, is only one of many processes influenced by climate change that could affect estuaries. Pritchard

(1967) defined an estuary as "a semienclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with freshwater derived from land drainage" (Chapters 1 and 2). Embodied within this definition is the fact that estuaries are expressions of interactions among land, river, and ocean processes. Therefore, any change in either the ocean or the watershed of the estuary due to climate change has the potential to affect estuaries. Also, climate change is currently affecting both the oceans (i.e., rising sea level) and watersheds (i.e., changes in freshwater runoff). In the first edition of Estuarine Ecology, climate change was a minor topic. But in the ensuing two decades, climate-change impacts on coastal ecosystems have become a major topic of research and policy. In this chapter, we review the evidence for climate change and future climate-change predictions, and the potential impacts that this change will have on estuarine ecosystems.

20.2 CLIMATE CHANGE: HISTORY AND PROJECTIONS

Changing climate and its potential impact on the biosphere and society have long been a topic of discussion. For example, it has been noted for decades that CO_2 levels in the atmosphere and global mean temperatures have been rising (Fig. 20.1a,b). Because of these concerns, the Intergovernmental Panel on Climate Change (IPCC) was established in 1988 by the World Meteorological Organization and the United Nations Environment Programme. The goal of the IPCC was to objectively synthesize a growing body of the technical climate-change literature into a format that was accessible to policymakers and scientists across disciplines. The panel consists of three ''working groups'' that assess, respectively, (i) the scientific aspects of climate change, (ii) the effects of climate change on socioeconomic and natural systems, and (iii) the options for reducing greenhouse gases and mitigating the effects of climate change. The IPCC produces a variety of special reports and technical papers, but the most anticipated and widely read publications are the comprehensive Assessment Reports published in 1990, 1996, 2001, and 2007. These peer-reviewed reports, the product of hundreds of experts from all three working groups, assess and synthesize the current scientific and socioeconomic literature concerning climate change. After years of consideration and analysis, the IPCC, in their 2007 assessment report, issued their strongest statement to date:

> Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level.

> Most of the observed increase in global average temperatures since the mid-twentieth century is very likely due to the observed increase in anthropogenic greenhouse gas concentrations.

In the next section, climate predictions by the IPCC and other studies are summarized.

20.2.1 Temperature

The IPCC predicts that, as atmospheric greenhouse gas concentrations increase (Fig. 20.1a), global temperatures will rise from 1 to 5 $°C$ during the twenty-first century. This compares to a rise of about 1$°$ in the twentieth century (Fig. 20.1b). By comparison, the mean global temperature increased by about 6 $°C$
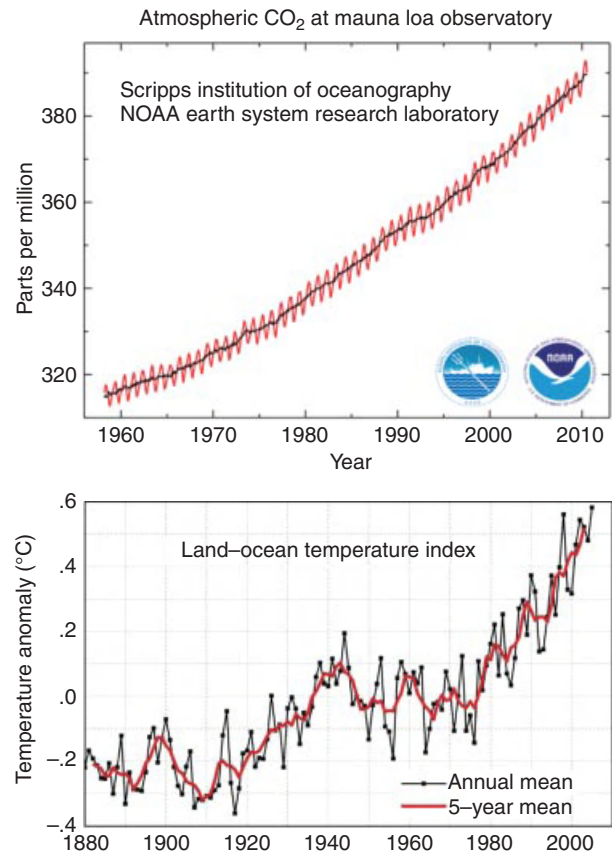
FIGURE 20.1 (a) Atmospheric carbon dioxide concentrations from Muana Loa, Hawaii as first measured by David Keeling starting in 1958. (Graph courtesy of Dr. Pieter Tans, NOAA/ESRL, www.esrl.noaa.gov/gmd/ccgg/trends.) (b) Global mean surface temperature change over the past century (Hansen et al., 2001; Reynolds and Smith, 1994; Rayner et al., 2003).

from the height of the ice age 15,000 years ago to about 5000 years ago when the oceans approached their present level. Thus, human activity may lead to a temperature increase of a similar magnitude in one century. Temperature directly affects many vital life processes, and a change in the thermal regime (extreme temperatures, their duration and seasonal rates of temperature change) can directly regulate rates of growth, reproduction, and migratory patterns of many species. Increasing temperature will also lead to changes in precipitation patterns and an acceleration of SLR and will likely affect tropical storm activity.

20.2.2 Sea Level Rise (Eustatic and Relative)

Sea level, as it appears to an ecologist standing in an estuarine wetland or to an individual *Spartina* plant

TABLE 20.1 SLR and estimated contributions from different sources (after IPCC, 2007)

	Rate of SLR (mm/year)	
	1961–2003	1993–2003
Actual observed rate of SLR	1.8 ± 0.5	3.1 ± 0.7
• Estimated contribution from sources		
• Thermal expansion	0.42 ± 0.12	1.6 ± 0.5
• Glaciers and ice caps	0.50 ± 0.18	0.77 ± 0.22
• Greenland ice sheet	0.05 ± 0.12	0.21 ± 0.07
• Antarctic ice sheet	0.14 ± 0.41	0.21 ± 0.7
• Sum of estimated contribtions[a]	1.1 ± 0.5	2.8 ± 0.7

Abbreviation: SLR, sea level rise.
[a]The sum of estimated contributions derived from various sources and methodologies do not necessarily add up to the actual observed rate of SLR.

growing in that wetland, is a function of both the volume of water in the ocean (the eustatic sea level) and the vertical displacement of the land surface due to processes such as subsidence or accretion (Rybczyk and Callaway, 2009; Nuttle et al., 1997). The apparent SLR in an estuary that results from both eustatic sea level rise (ESLR) and vertical land displacement is referred to as *relative sea level rise* (*RSLR*).

Eustatic sea levels rise and fall as a function of long-term climate variation. During cold periods, water is locked up in land-based glaciers and ice caps, and sea levels are relatively low. For example, during the last glacial maximum, which ended approximately 18,000 years ago, sea levels were more than 100 m below current levels (Valiela, 2006) and have been rising ever since (Chapter 2). In addition, under a regime of global warming, the volume of water in the ocean expands as the ocean itself warms. Currently, a little more than half of the observed ESLR is due to this thermal expansion (Table 20.1).

Recent observations have revealed an ESLR rate of 1.8 mm/year for the period 1961–2003, and a rate of 3.1 mm/year for the period 1993–2003, compared to the background rate of 1–2 mm/year for the nineteenth and early twentieth century (Fig. 20.2; Meehl et al., 2007). Although it is generally agreed that the rate of ESLR will increase in the future, predicting the exact future rate of SLR is uncertain because it is a function of numerous complex processes, both physical (e.g., the thermal expansion of water and the melting of glaciers and ice caps) and political (e.g., future carbon emissions; Fig. 20.3; Rybczyk and Callaway, 2009).

The IPCC (Meehl et al., 2007) predicts that sea level will rise by 18–59 cm by the end of the twenty-first century, with a best estimate of about 40 cm (Fig. 20.4). However, many feel that this estimate is conservative. For example, the observed rate of
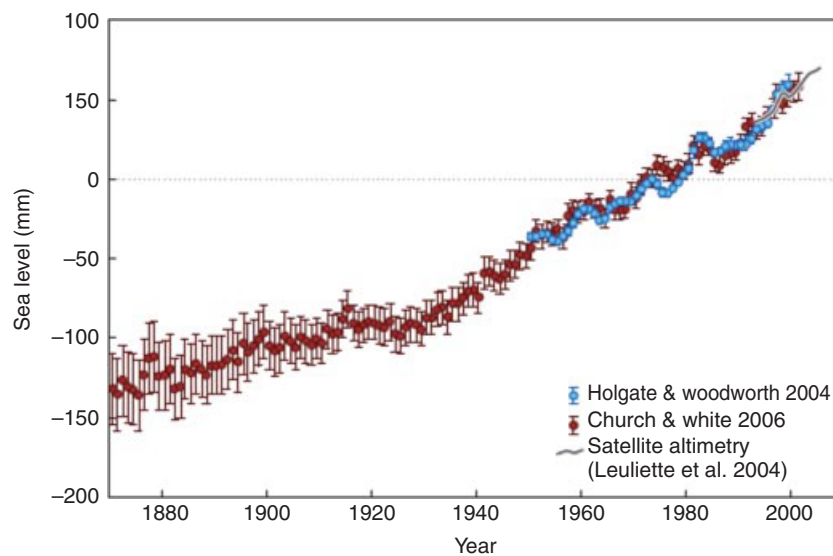
FIGURE 20.2 Annual averages of global mean sea level from the IPCC (2007). The red data are updated from Church and White (2006), the blue data are from Holgate and Woodworth (2004), and the gray curve is based on satellite altimetry form Leuliette et al. (2004). Error bars show the 90% confidence limits. Zero represents the 1961–1990 averages for red and blue data (Fitzgerald et al., 2008, with permission).
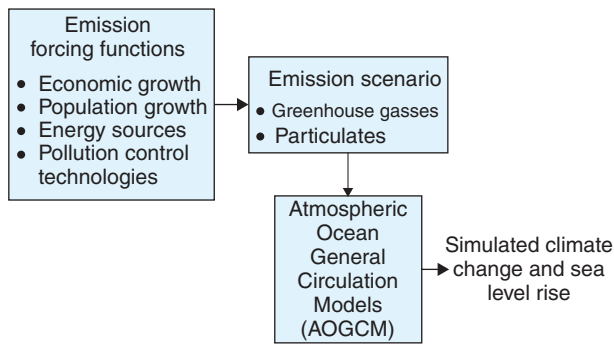
FIGURE 20.3 Human and physical dimensions to predicting future rates of sea level rise.

ESLR from 1993 to 2003 has already exceeded the lower limit predicted by the fourth IPCC assessment. A number of recent studies suggest that ESLR will likely be a meter or more (Rahmstorf, 2007; Pfeffer et al., 2008; Rohling et al., 2008; Mitrovica et al., 2009; Vermeer and Rahmstorf, 2009). These conclusions are based on temperature–SLR relationships in the twentieth century and a better understanding of ice sheet dynamics in a warming world. Most glaciers have retreated significantly in the twentieth century.

RSLR is the combination of ESLR and subsidence. Where there are high rates of subsidence, RSLR can be much greater than ESLR. High rates of geological subsidence commonly occur in deltas because of compaction, consolidation, and dewatering of sediments. Compared to ESLR of 1–2 mm/year for the twentieth century, RSLR for the Mississippi delta was in excess of 10 mm/year (Baumann et al., 1984; Day et al., 2007). RSLR in the Nile delta region is as high as 5 mm/year (Stanley, 1988; Milliman et al., 1984) and is between 2 and 6 mm/year for the Rhone and Ebro deltas (Sestini, 1992; Ibáñez et al., 1996; Pont et al., 2002). Humans have accelerated RSLR by drainage and withdrawal of water, oil, and gas (Sestini, 1992; Morton et al., 2002; Ko and Day, 2004). An understanding of vegetation response in areas with high RSLR can provide insights into the effects of accelerated ESLR
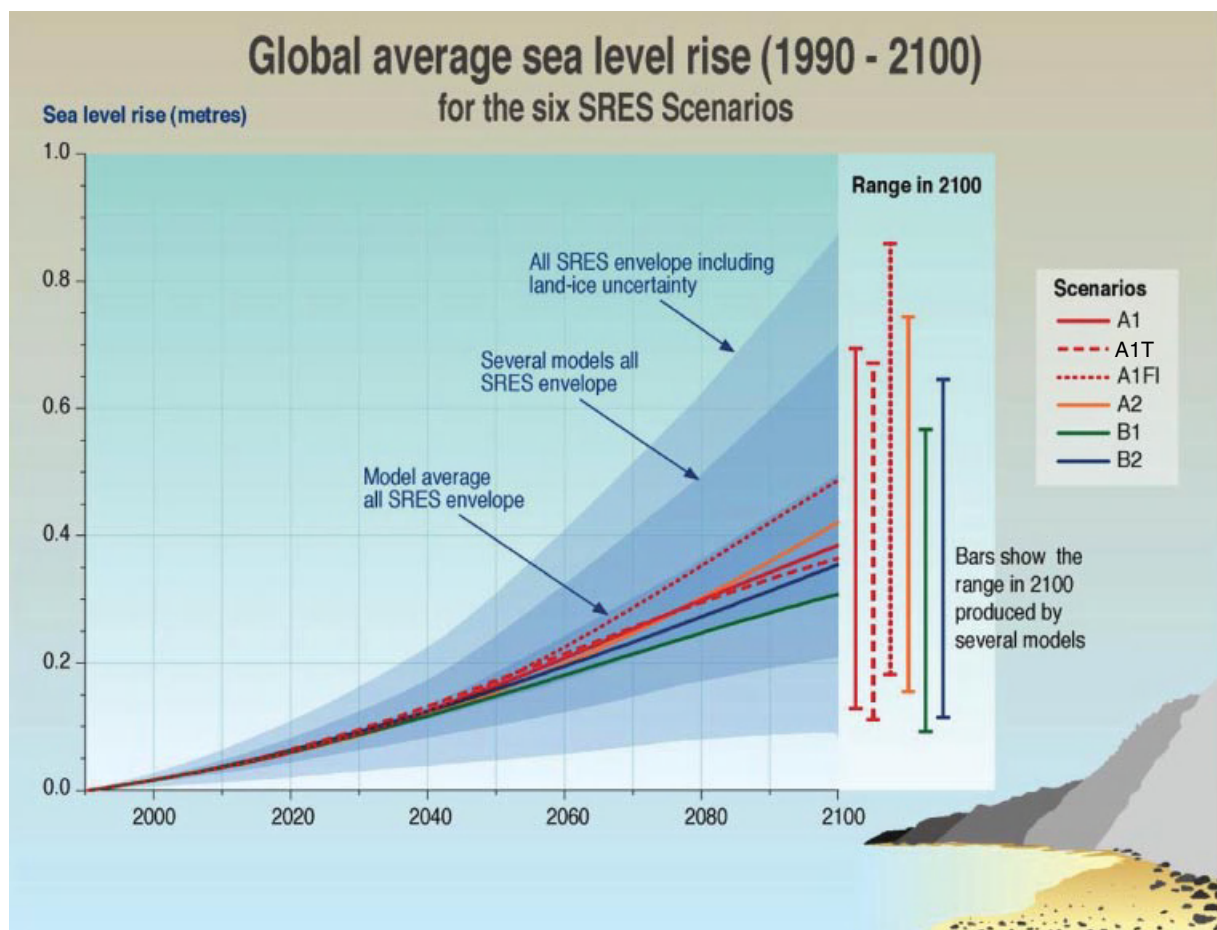
FIGURE 20.4 Predicted global mean sea level rise through 2100 (Meehl et al., 2007).

in the future (Stanley, 1988; Day and Templet, 1989; Stevenson et al., 1985; Day et al., 1997, 2005, 2007; Pont et al., 2002). What are the limits to accretion of coastal wetlands and how may human activities affect this accretion? This question is addressed in a later section.

As an aside, in any discussion of wetland elevation relative to sea level, there is often ambiguity regarding the terminology itself. The term *SLR* alone is ambiguous as it could refer to the absolute rise in sea level (i.e., ESLR), or the apparent rise caused by both ESLR and land subsidence. Similarly, land subsidence could include deep geologic subsidence, shallow subsidence caused by compaction and organic matter decomposition, or both. The terms used in this chapter are defined in Table 20.2.

20.2.3 Changes in Storm Frequency and Intensity

Increasing warming of surface waters of the oceans suggests that there may be an increase in the frequency of tropical cyclones and hurricanes (Raper, 1993; Walsh, 2004), but there has been much uncertainty in such predictions (Henderson-Sellers et al., 1998; Wigley, 1999). Recent reports, however, have drawn stronger conclusions concerning storms and climate change. Emanuel (2005) reported that sea surface temperatures in the tropics increased by about $1\degree$C over the past half century, and during the same period, total hurricane intensity or power increased by about 80%. This increase in intensity was due both to more powerful storms and to an increased duration of these storms. Webster et al. (2005) reported an increase in the number of category 4 and 5 storms over the past several decades. It has been argued

that these increases in storm intensity, strength, and duration are not linked to climate change but are due to decadal cycles in tropical storm activity. Hoyos et al. (2006), however, analyzed factors contributing to hurricane intensity and concluded that the increasing numbers of category 4 and 5 hurricanes for the period 1970–2004 was directly linked to the increase in sea surface temperatures. Elsner et al. (2008) also concluded that there was an increasing intensity of the strongest tropical storms. Regardless of whether the recent intensification of hurricanes is due to climate change or is part of a decades-long cycle, it is likely that there will be more and stronger hurricanes in the coming decades and this will interact with other climate forcings to impact estuarine ecosystems. Changes in the intensity and frequency of storms can have a variety of impacts, especially on coastal wetlands, as outlined below.

20.2.4 Freshwater Input, Sediment Transport, and Nutrient Delivery

Changes in precipitation patterns will result in changes in freshwater flow to the coastal zone. In general, IPCC climate models predict that precipitation will increase in the moist tropics close to the Equator, decrease in subtropics and mid-latitudes, and increase at higher levels (Fig. 20.5a). These changes in precipitation will lead to changes in freshwater runoff (Fig. 20.5b). Changes in precipitation are strongly site specific and highly variable, but some model results indicate that the Mediterranean and Mid East, southern Africa, large parts of Australia, and much of the US southwest and northwest Mexico will experience much lower freshwater runoff. There is uncertainty in these predictions, but there is no

TABLE 20.2 Definition of terms associated with the measurement of relative sea level

Term	Definition
Accretion	Surface vertical accumulation of mineral and organic sediment, usually over some marker horizon. May also integrate processes occurring on and within the upper part of the marsh substrate (e.g., root growth)[a]
Shallow subsidence	Primary compaction, decomposition, and dewatering that occur in upper sediments (up to 10 m)[a]
Deep subsidence	Deep primary compaction, secondary compaction, and other processes such as geosynclinic downwarping and tectonic activity[a]
Eustatic sea level rise	Global sea level rise caused by changes in the volumes of glaciers and ice caps and by water density/temperature-dependent relationships [a]
Relative sea level rise	Long-term, absolute, vertical relationship between the land and water surface. On the marsh surface, RSLR should be calculated as ESLR + deep subsidence + shallow subsidence. However, RSLR measured using tidal gauge records represents only ESLR + deep subsidence
Net accretion balance	= Accretion - shallow subsidence − deep subsidence − ESLR or = Accretion − RLSR

Abbreviations: ESLR, eustatic sea level rise; RSLR, relative sea level rise.
[a]Cahoon et al. (1995).

(a)

Projected patterns of precipitation changes

Multi–model   A1B   DJF multi–model   A1B   JJA

©IPCC 2007: WG1-AR4

(b)

5: Electricity production potential at existing hydropower stations decreases by more than 25% by the 2070s

4: Flooded area for annual peak discharge in bangladesh increases by at least 25% with a global temperature increase of 2°C

2: Streamflow decreases such that present water demand could not be satisfied after 2020, and loss of salmon habitat

6: Increase of pathogen load due to more heavy precipitation events in areas without good water supply and sanitation infrastructure

1: Thickness of small island freshwater lens declines from 25 to 10 m due to 0.1 m sea level rise by 2040-2080

3: Groundwater recharge decreases by more than 70% by the 2050s

FIGURE 20.5 (a) IPCC expected climate-change impacts on rainfall by the end of the century (blue denotes relative increase and red denotes relative decrease). (b) Expected climate change impacts on water runoff by the end of the century (Meehl et al., 2007).

doubt that they will impact estuarine ecosystems. These changes will bring about respective decreases and increases in sediment and nutrient input to estuaries. The degree to which these alterations in supply are affected depends on both the degree to which humans control the flow of water to the coast and our management of land and waters. An interesting example of the complexity of this issue is the Mississippi River and delta. The IPCC models suggest that there may be lower local freshwater runoff along the northern coast of the Gulf of Mexico. However, over 90% of Mississippi discharge is derived from the upper Midwest and Ohio basins.

Some models predict that river discharge will increase by up to 40% by 2100 (i.e., Day et al., 2005). This will complicate management of the Mississippi delta. But it is possible that extra-Mississippi flow can be used to offset periodic droughts in the delta. A similar situation exists for the north central Mediterranean. The Mediterranean is expected to dry but the Rhone River may increase in discharge since much of its flow is derived from the central part of France where rainfall is predicted to increase or remain about the same.

Table 20.3 summarizes observed and predicted indicators of climate change that likely strongly

BOX 20.1   The effects of climate change on estuarine dependent species: pacific northwest salmonids: a case study

Salmon are certainly a cultural and economic icon of the Pacific Northwest (PNW). Historic spawning runs in the Columbia River, for example, once numbered in the millions (Fig. 20.6). Unfortunately, overfishing, pollution, habitat modification and loss, and dam construction over the past 150 years have greatly reduced salmon population in the PNW (Meengs and Lackey, 2005). The Environmental Protection Agency (EPA) currently lists nine genetically distinct stocks of Chinook Salmon on the West coast as either threatened or endangered.

FIGURE 20.6   Salmon at a Seattle, WA cannery around 1900. Some studies suggest that climate change will further reduce already decimated populations (University of Washington Libraries, Special Collections, Negative #A. Curtis 27678).

In general, there are six recognized salmon species in the PNW; Chinook (*Oncorhynchus tshawytscha*), Chum (*Oncorhynchus keta*), Coho (*Oncorhynchus kisutch*), Pink (*Oncorhynchus gorbuscha*), Sockeye (*Oncorhynchus nerka*), and Steelhead Trout (*Oncorhynchus mykiss*). Because they are anadromous (they return to freshwater streams and rivers to spawn after spending their adult life in the ocean; Fig. 20.7), any change in freshwater stream flow, estuarine habitat, or ocean conditions, due to climate change has the potential to negatively affect population levels.

All salmon species use estuaries to some extent for migration, adult residence, or juvenile rearing (Williams and Thom, 2001), none more so than the Chinook, which may spend up to 6 months in estuaries as juveniles. Indeed, recent studies have linked the survival of Chinook salmon, at least, to pristine estuarine habitat in the PNW (Magnusson and Hilborn, 2003). Any loss of estuarine habitat due to SLR (Section 20.3.2) then has the potential to reduce population levels. For example, Hood (2005) estimated that, for an SLR of 45 cm, juvenile Chinook salmon in the Skagit River Delta, the largest river flowing into the Puget Sound, would decline by 211,000 fish because of habitat loss. Rising sea levels could also inundate estuarine and beach spawning habitat for the forage fish on which salmon depend (Glick et al., 2007).

Finally, many salmon streams in the PNW are dependent on a winter snowpack in the mountains to provide adequate flow in the summer. Regional climate-change models predict more winter precipitation will fall as rain and less as snow for the PNW, leading to reduced winter snowpack, lower summer stream flows that are dependent on that snowpack, higher summer temperature under a low summer flow regime, and increased fall and winter flooding. All of these scenarios have the potential to negatively affect salmon population (Fig. 20.7).

FIGURE 20.7 Sea level rise due to climate change can directly affect salmon populations by reducing critical estuarine habitat. In addition, the red boxes explain how changes in stream temperature and flow may also affect salmon during various phases of their life cycle. *Source:* Casola et al. (2005), modified from Wilderness Society (1993).
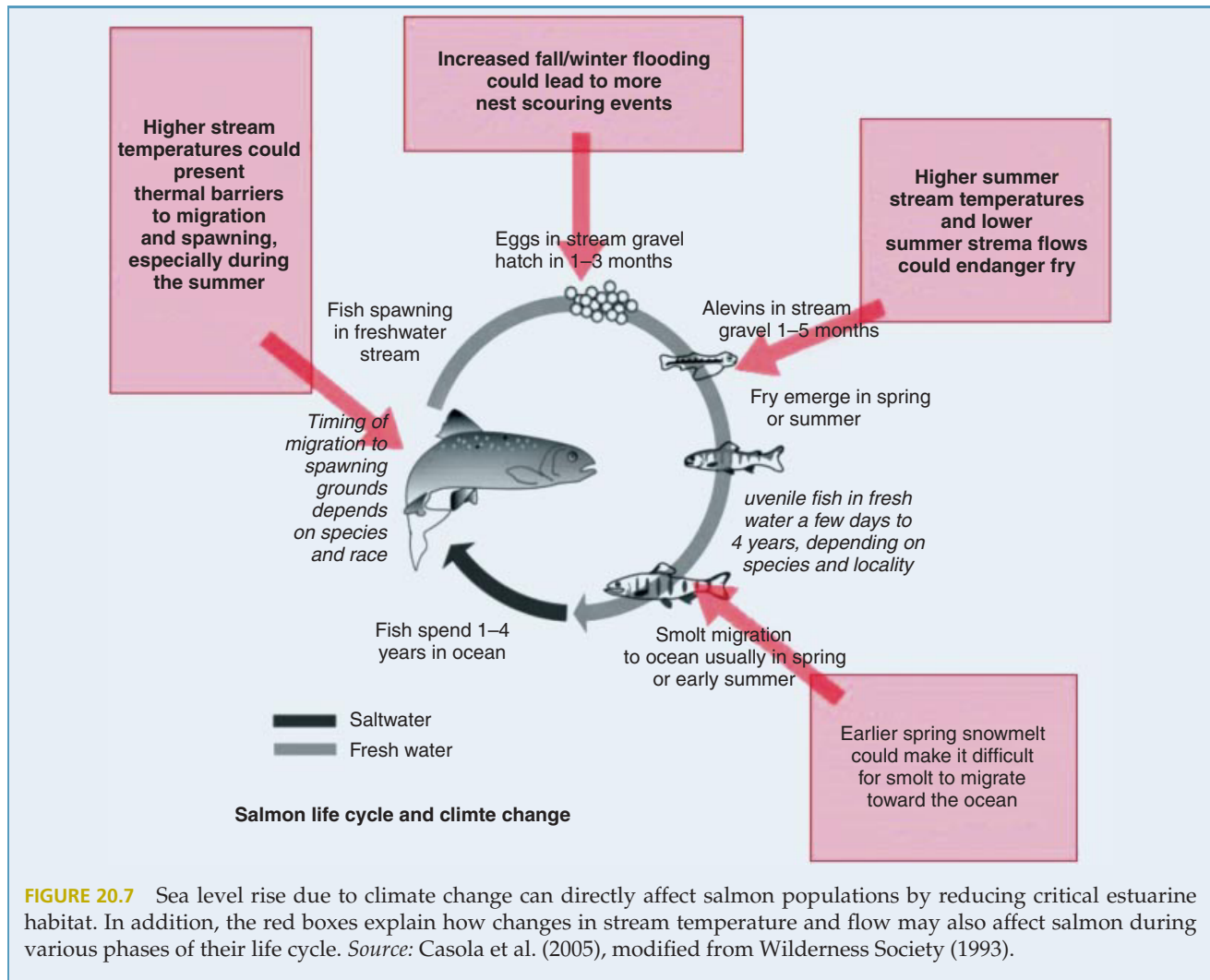
impact estuarine ecosystems. In the second part of this chapter, these climate impacts on estuarine ecosystems are discussed.

20.3 EFFECTS OF CLIMATE CHANGE ON ESTUARINE ECOSYSTEMS

What then are the impacts to estuaries of these current and predicted changes in climate? These are addressed in the following sections.

20.3.1 Temperature

Strong geographic gradients in temperature exist from the tropics to the poles. Many species, such as mangroves, have thermal niches that allow them to inhabit only portions of these temperature gradients. Correspondingly, climate-induced changes in regional temperature regimes will almost certainly induce a wide range of ecological responses, ranging from local extinction of individual species and changes in biodiversity to changes in the rates of ecosystem processes, such as primary production and bacterially mediated decomposition. Net primary production of some estuarine species, the sea grass *Zostera marina*, for example, may decrease as leaf respiration rates increase more rapidly than photosynthesis rates with increasing temperature (Short and Neckles, 1999). Many species will shift their geographic ranges to the north. One of the most interesting areas to study the effects of temperature is the tropical–temperate interface. In the Gulf of Mexico, for example, much of the northern Gulf has been

TABLE 20.3 **Some indicators of climate change that could affect estuarine systems**

Selected Indicator[a]	Observed Changes in the Twentieth Century	Predicted Changes in the Twenty-First Century
Atmospheric concentration of CO_2	Increased from 280 ppm for the period 1000–1750 to 379 ppm in year 2005[a]	Projected concentrations range from 490 to 1250 ppm by the year 2100[b]
Global mean surface temperature	Increased by $0.74 \pm 0.2\,^{\circ}$C for the period 1906–2005[a]	For the next two decades (2007–2027), a warming of $0.2\,^{\circ}$C is projected[a]
Continental precipitation	Increased by 5–10% over the twentieth century in the Northern Hemisphere, although decreases were observed in some regions[b]	Globally, an increase of 5–20% during the twenty-first century although, regionally, there will be both increases and decreases. Larger year-to-year annual variation[a]
Heavy precipitation events	Frequency of events increased over most land areas[a]	More intense precipitation events are very likely (90% probability of occurrence).[a]
Frequency and severity of drought	More intense and longer droughts over wider areas since the 1970s, especially in the tropics and subtropics[a]	Areas affected by drought likely to increase and be concentrated in mid-latitudes[a]
Global mean sea level	Total twentieth century rise of 0.17 mm/year (0.17 m), with an observed increase in this rate to 3.1 mm/year since 1993[a]	A rise of 0.18–0.59 m by 2099. These projections do not include a possible future increase in the rate of ice flow from Greenland and Antarctica.[a] Recent studies suggest a meter of more rise
Snow cover	Decreased in area by 10% since global observations became available in the 1960s.[b]	Continued decrease in winter snowpack[a]
El Niño events	Became more frequent, persistent, and intense during the past 20–30 years (1970–2000) compared to the previous 100 years[b]	Many models predict an increase in El Niño events[b]
Nonpolar glaciers	Widespread retreat during the twentieth century[a]	Continued retreat over the next 100 years[b]
Tropical and extratropical cyclone activity	Likely increase in activity since 1970[a]	Likely increase in intensity (wind speed and precipitation)[a]

[a] IPPC summary for policymakers report (2007).
[b] IPPC summary for policymakers report (2001).

dominated by salt marshes with mangroves occurring in south Florida, sporadically in the Mississippi delta, and from south Texas into the southern Gulf. In the twenty-first century, it is highly likely that the entire coastal zone of the Gulf of Mexico will become tropical (Day et al., 2012a).

20.3.2 Accelerated Sea Level Rise

Of all climate-change-related threats to estuaries, perturbations caused by rising sea levels are certainly the most obvious and the most studied. Undoubtedly, this is because the dramatic effects of high rates of relative SLR have already been observed in regions such as coastal Louisiana (Day et al., 2007) where high rates of land subsidence combined, with rising eustatic sea levels, led to wetland loss rates of 60 km²/ year in the 1980s and 1990s (Boesch et al., 1994; Fig. 6.13). Indeed, observed and predicted increases in

the rate of ESLR have led to concerns regarding the resiliency of coastal wetlands worldwide (Reed, 1995), the essential questions being: how will estuarine habitats change and can wetland elevation keep pace with rising sea levels?

Estuarine wetlands exist in a dynamic equilibrium between the forces that lead to their establishment and maintenance, such as sediment accretion, and the forces that lead to their deterioration, such as increasing rates of ESLR and subsidence (Day et al., 1999). Changes in either side of the maintenance/deterioration equation could lead to changes in the inundation regime, anaerobic stress levels throughout the wetland, and shifts in habitat types.

As sea levels rise, estuarine wetlands can respond in one of three ways. First, they can accrete sediments at a rate that equals the rate of SLR, resulting in no net change in habitat area or type. Estuarine wetland elevation, relative to sea level, is
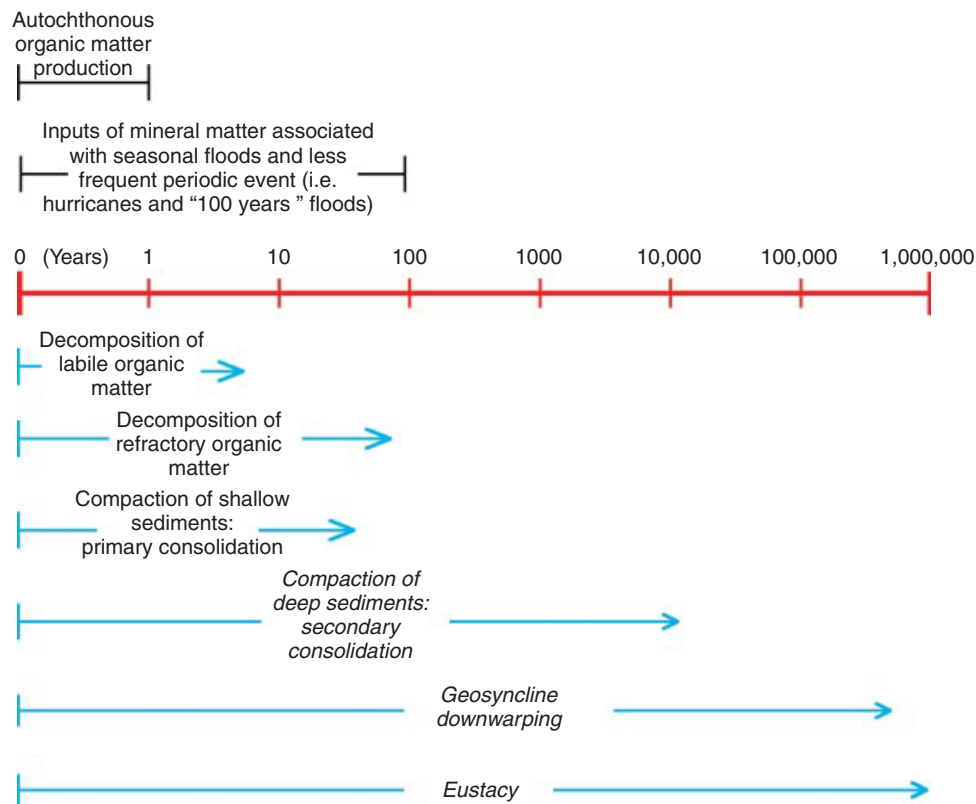
FIGURE 20.8 Processes that affect wetland elevation relative to sea level rise. Processes shown below the time line decrease elevation, whereas those shown above increase elevation. Processes shown in italics are commonly entered as forcing functions into existing wetland elevation models.

a function of numerous processes including mineral and organic matter accretion, sediment compaction, deep subsidence, and ESLR, all operating at different timescales (Fig. 20.8). A number of studies have shown that estuarine wetlands can persist for long periods of time (thousands of years) in the face of rising sea levels when sediment accretion equals or exceeds the rate of land subsidence plus ELSR, as is the case for most wetlands worldwide under current rates of ESLR (Gornitz et al., 1982; Redfield, 1972; McCaffrey and Thompson, 1980; Orson et al., 1987; Morris et al., 2002; Rybczyk and Cahoon, 2002).

The rate at which vertical accretion occurs is a function of the combination of the inputs of both inorganic and organic material to the soil (Fig. 20.8). Organic material is mostly derived from the growth of plant roots, whereas inorganic material is mostly supplied in the form of sediments that come from either sea- or freshwater sources. Many rivers flowing into estuaries now carry only a fraction of the inorganic sediment that they did historically because of reservoir construction (Po, Ebro, and Nile). For example, sediment discharge to the Mississippi delta has decreased by at least 50% since 1860 (Kesel, 1989;

Meade, 1995). Recent work indicates that much of the deltaic wetlands will disappear because of the combination of RSLR and reduced sediment input (Chapter 19).

Second, estuarine habitat can migrate upslope as sea levels rise. At the wetland–upland transition, there could be conversion of upland areas to wetlands as wetlands "migrate" inland (Brinson et al., 1995). However, in many locations, coastal wetlands are bordered by development or steep habitats such that migration would not be possible (Titus, 1991), in which case remaining habitat would be slowly "squeezed" out of existence.

Finally, if wetlands cannot keep pace with rates of SLR, an increase in inundation frequency and duration could lead to a shift in the distribution of vegetated habitats across a wetland (Warren and Niering, 1993; Kirwan and Murray, 2008; e.g., shifts from areas dominated by *Spartina patens* to *Spartina alterniflora*). Over longer time periods, these types of changes would lead to conversion of more and more wetland area to unvegetated mudflats or even subtidal open water as happened in the Mississippi delta.

BOX 20.2   Measuring the processes that affect wetland elevation

While many coastal wetlands accumulate sediment at a rate that keeps pace with current rates of ESLR, the focus of most managers presently, and especially in the future, is and will be on the loss of relative elevation and the submergence of tidal wetlands due to increased rates of ESLR. The potential for coastal wetland submergence has traditionally been determined by calculating a net accretion balance (Table 20.2). This is accomplished by comparing rates of vertical accretion to rates of RSLR (ESLR plus deep subsidence). Rates of accretion are typically estimated by measuring the accumulation of sediments, both organic and mineral, over some known and dated marker horizon such as feldspar clay, ^{137}Cs or ^{210}Pb. Estimates of deep subsidence are usually based on long-term records from tide gauges that are mounted on stable piers, bridges, or pilings that extend through the shallow subsidence zone (and thus do not include shallow subsidence). A tidal gauge record spanning at least 18.6 years is required to factor out variations because of the Moon's nodal cycle (Turner, 1991). Typically, mean annual or monthly water levels are regressed against time to yield a rate of RSLR. To estimate the deep subsidence component of RSLR, current ELSR is subtracted from the water level rise recorded from the pier-mounted tide gauge. ESLR is derived from the analysis of tide gauge data from coasts worldwide that are assumed to be geologically stable (Penland and Ramsey, 1990) or, more recently, from satellite data.

Recent research has shown that the compaction in the upper 5–10 m of sediment contributes a shallow component that is often overlooked when calculating RSLR (Cahoon et al., 1995). This results in an underestimation of the accretion balance. Shallow subsidence is the result of primary sediment consolidation and the decomposition of organic matter (Table 20.2). It is an especially important process in coastal systems under stress (e.g., from flooding or salt) where below ground plant structures, such as roots and rhizomes, die and decompose, leading to rapid subsurface collapse (Cahoon et al., 2003). It is also an active process in coastal systems that are rapidly accreting, such as deltas, as surface sediments consolidate (Day et al., 1999). In the Mississippi River delta, for example, high rates of RSLR in the coastal marshes have lead to increasingly long periods of flooding, plant mortality, and rates of shallow subsidence that sometimes exceed 2.5 cm/year.

To this end, surface elevation tables (SETs) have been widely used for measuring both changes in elevation and shallow subsidence in coastal estuaries.

The SET was introduced from the Netherlands into the United States in the early 1990s by Boumans and Day (1993) and is now widely used for measuring coastal wetland elevation dynamics as it relates to SLR (Cahoon et al., 1995). The SET is a portable leveling device that is attached to a permanent benchmark pipe or rod driven to the point of refusal into the marsh sediments (Fig. 20.9) and provides a fixed reference position from which precise changes in elevation (within millimeters) can be measured (Cahoon et al., 2003). At any one point in time, the distance from the fixed SET to the marsh surface is measured by lowering a set of pins (usually nine) from the SET to the marsh surface (Fig. 20.9). Furthermore, the SET can be rotated around several fixed positions (usually four or eight) on the benchmark pipe or rod, allowing for up to 9×8 precise measurements. Repeated measurements, from exactly the same positions, yield change in elevation over time. SETs are especially useful when used simultaneously with feldspar marker horizons, or other methods that measure recent sediment accretion, because it allows for the estimation of shallow subsidence (Fig. 20.9).

However, for several reasons, these calculations must be viewed with caution to determine accretion balances even if shallow subsidence is considered. First, short-term field measurement does not necessarily integrate long-term processes that affect wetland elevation, such as compaction, decomposition, and pulsing events such as storm-related sediment deposition (i.e., Day et al., 1999). Even programs that span a decade or more may not capture infrequent sediment deposition events from hurricanes or major river floods (Rybczyk and Cahoon, 2002). Second, these types of measurements may not take into account possible feedback mechanisms on the processes themselves. For example, a change in elevation typically alters flooding patterns that can, in turn, affect rates of sediment deposition, decomposition, and autogenic primary production. Over time, these measured rates change in a nonlinear manner. Finally, the direct comparison of rates of elevation change with rates of RSLR can be problematic because of the large amount of uncertainty involving measurements of the processes affecting marsh elevation and SLR. For these reasons, a simulation model that considers all of the relevant processes over appropriate timescales, incorporates feedback mechanisms, and has methodologies for dealing with uncertainty (i.e., sensitivity analysis) can be a complimentary tool for examining the response of wetland elevation to increasing rates of SLR (Day et al., 1999; Rybczyk and Cahoon, 2002).
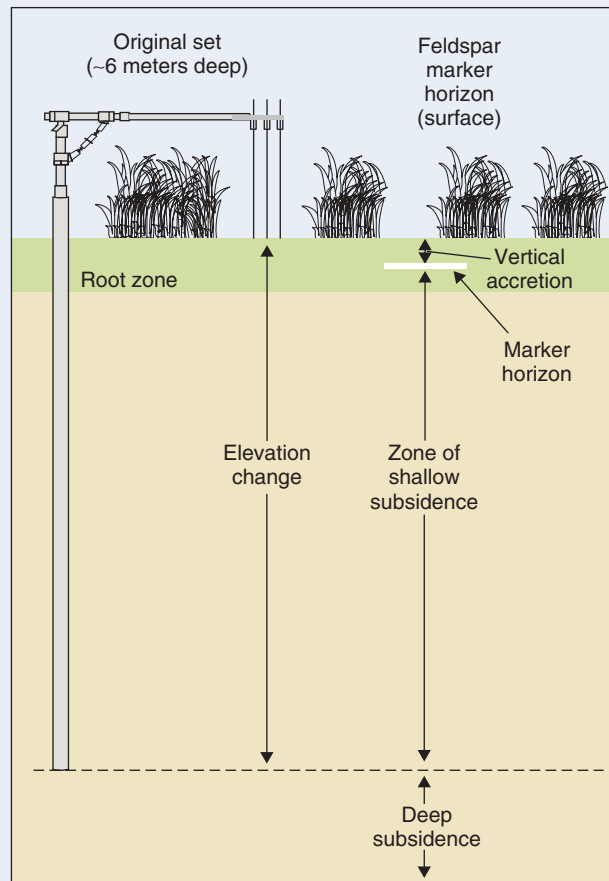
FIGURE 20.9 The original surface elevation table shown here being used in conjunction with a feldspar marker horizon. When used simultaneously, shallow subsidence can be calculated as change in elevation (as measured by the SET) minus accretion (as measured by feldspar marker horizon). Figure courtesy of J. Lynch, USGS.

SLR during the twenty-first century may strongly affect low-lying wetlands, such as the Mississippi and other deltas. Deltas are particularly susceptible because of their high RSLR rate. In some major deltas, subsidence will be as high as predicted ESLR in the twenty-first century. In parts of the Mississippi delta, for example, RSLR may exceed 2 m by the end of the century if ESLR of 1 m or more occurs. Because of the high rate of RSLR, deltas serve as models of the response of coastal systems generally to ESLR (Day and Templet, 1989; Day et al., 1997; Pont et al., 2002).

SLR has already led to significant geomorphological changes of coastal systems, salinity intrusion in estuaries, and loss of associated wetlands around the world, including Chesapeake Bay (Stevenson et al., 1985) and other mid-Atlantic estuaries (Kana et al., 1986; Hackney and Cleary, 1987), Long Island Sound (Clark, 1986), the Mississippi delta (Salinas et al., 1986; Conner et al., 1989; Day et al., 2000, 2007), the Grijalva/Usumacinta delta in the southern Gulf of

Mexico (Ortíz-Pérez et al., 2010), Rhone (Pont et al., 2002), Nile and Ganges (Stanley, 1988; Milliman et al., 1984), Indus(Snedaker, 1984) and Ebro (Ibáñez et al., 1996, 1997; Day et al., 2011) deltas, and Venice Lagoon (Pirazzoli, 1987; Sestini, 1992, 1996; Bondesan et al., 1995; Day et al., 1999).

Two important physiological reasons that lead to the loss of wetlands are flooding stress because of increased flooding duration and salinity stress (Mendelssohn and Morris, 2000; Chapter 6). Global climate change will likely exacerbate both of these stresses. Accelerated SLR will lead to significant increases in flooding duration. For example, Morris et al. (2002) developed, and later generalized (Morris, 2006), a theoretical feedback model that predicts change in salt marsh plant production and elevation in response to SLR. Their simulations and field work revealed that the optimal rate of SLR maximizes sediment accretion and productivity and also represents the upper limit of flooding tolerance for a given plant

BOX 20.3 Modeling the effects of SLR on coastal systems (Rybczyk and Callaway, 2009)

Given the complexity of estuarine systems, the timescales involved, and feedbacks between the many processes that contribute to wetland sustainability in the face of SLR, researchers have turned to computer modeling to explore and predict long-term wetland sustainability in the face of climate change. Over the past 25 years, a variety of coastal wetland/estuarine models have been developed to address the relationships between climate change, SLR, and coastal wetland sustainability. They differ in the spatial scales that are considered and the processes that are simulated within the model, as opposed to processes that are input as forcing functions or not considered at all. Forcing function is an independent input variable that drives a model but is not modified by the model itself; it is a variable that is not simulated. Although there is overlap, these models can be divided into three groups: (i) landscape models that simulate processes over large regions (i.e., entire estuaries or coastlines), (ii) geomorphic and ecogeomorphic models that simulate physical and ecological processes across a marsh platform or transect, and (iii) zero-dimensional models that simulate the change in elevation at one point rather than across an entire marsh.

In general, landscape models excel at simulating general trends at large special scales but often do not mechanistically simulate the many processes that affect the system (in other words, many of the processes are input as forcing functions and are not simulated within the model). In one of the first efforts of this type, Park et al. (1989) developed a model SLAMM2 (Sea Level Affecting Marsh Model) that was used for 93 sites and predicted changes in land classes based on elevation, erosion, surrounding land type, accretion rates, and inundation. Modified versions of the SLAMM model are still used for assessing landscape-scale impact of SLR on coastal systems (Clough and Park, 2006). Other types of landscape-scale models are linked to complex and computer-intensive oceanographic hydrodynamic models that simulate changes in sea level, salinity, and sediments (Martin et al., 2000; Reyes et al., 2000). Changes in habitat type are simulated by simple switching functions that are dependent on these three parameters.

At the other end of the spatial scale are the zero-dimensional wetland models or "point" models that simulate change in relative wetland elevation, for example, for one specific point in a coastal wetland. Early zero-dimensional models tended to focus on either mineral deposition or organic sediment processes, although there is now overlap between the two. One of the first of these models was developed by Krone (1987) for San Francisco Bay. The model was designed to evaluate the historic location of the mean high water datum by simulating changes in wetland elevation over time. Krone mechanistically simulated mineral accretion rates based on predicted periods of tidal inundation combined with assumptions concerning concentrations and settling rates for suspended sediments. The model was calibrated with ^{14}C data, and Krone found that the accretion rate increased with higher rates of SLR. The method that Krone developed is, to this day, the general approach that is used for mechanistically simulating mineral sediment dynamics in most wetland elevation models. These groups of models lack horizontal spatial articulation, but they excel at simulating site-specific processes in a mechanistic manner.

Spanning the gap between zero-dimensional models and regional-scale landscape models are the geomorphic models that simulate morphodynamics (i.e., sedimentation, channel development, and erosion) across a marsh platform (a two-dimensional model) or a marsh transect (a one-dimensional model). These models are said to be "ecogeomorphic" or "biogeomorphic" if they additionally consider the feedbacks between marsh vegetation and physical processes such as sedimentation and erosion. Since many of the processes that affect wetland elevation, such as sedimentation rates, vary across the marsh surface, these types of models have recently been used to examine the response of salt marshes and tidal flats to SLR (Kirwan and Murray, 2007). These models emphasize the physical processes that affect marsh surface topography and typically include mechanistic algorithms that describe wave energy, tidal currents, shear stress, and sediment erosion. Ecogeomorphic models also consider how marsh biota influences these physical processes, especially rates of deposition and erosion. In one of the most recent efforts to simulate the effects of SLR on marsh wetland elevation, Kirwan and Murray (2008) developed an exploratory, ecogeomorphic model for Westham Island, a salt marsh/tidal flats system in the Fraser River Delta, British Columbia. The model uses modification of the deposition algorithm from Morris et al. (2002) that accounted for distance from tidal channels, simulated wave height and wave-induced erosion, and linked marsh elevation to a simple plant productivity switching function (i.e., plant productivity decreased with decreasing elevation). It also incorporated a sediment deposition/elevation/plant productivity feedback function (plant productivity affects

sediment deposition rates that, in turn, affect elevation, which influences plant productivity). Output was generated as two-dimensional elevation and vegetation zone maps of the island under various SLR scenarios. They found that an RSLR of 1.036 m in the next 100 years resulted in a loss of approximately 38% of total vegetated area.

Models of all types can be used to predict how rising sea levels will affect and change estuarine habitat and to determine what types of habitats and estuaries are most vulnerable to SLR. As models become more sophisticated and site specific, they can be used by coastal managers to guide the course of restoration efforts in a given estuary.

species. The model predicted that their study site, a *S. alterniflora* marsh in South Carolina, could tolerate a rate of RSLR of up to 1.2 cm/year.

Rising sea level combined with lower freshwater input may lead to increased saltwater intrusion and salinity stress in areas experiencing lower freshwater input. This especially threatens areas where there are extensive tidal freshwater wetlands such as in deltas. This combination of high RSLR, increased temperature, and lower freshwater input makes the Mississippi and other deltas highly vulnerable to climate change (Thieler and Hammar-Klose, 2001; Syvitski et al., 2009).

20.3.3 Freshwater Input on Coastal Ecosystems

Increased freshwater input can have both beneficial and detrimental impacts on coastal systems. The benefits of freshwater input stimulating vertical soil accretion have already been highlighted. An additional benefit is increased fisheries production in coastal systems (Nixon, 1988), and this is addressed in the next section. This results because the nutrients in freshwater flowing into estuaries stimulate primary production, which, in turn, increases the energy available for organisms that fish forage on.

One negative impact associated with the increase in freshwater runoff to coastal ecosystems is an excessive increase in nutrients. There is already considerable evidence that agricultural runoff and sewage wastewater from human activity in tributary watersheds is degrading many coastal ecosystems in the Gulf of Mexico and elsewhere. Nuisance algal blooms and low oxygen in bottom waters kill fish and shellfish, as has been well documented in Chesapeake Bay (Harding and Perry, 1997; Kemp et al., 1992) and has been suggested for the coast of Louisiana in the so-called Gulf Dead Zone (Rabalais et al., 1996) as well as worldwide (Diaz et al., 2008). Recently, however, Breitburg et al. (2009) concluded that hypoxia does not typically reduce fisheries in coastal systems. A num-

ber of management suggestions have been made to reduce high nutrient loading to streams and coastal waters. For the Mississippi River basin, for example, these recommendations include changes in farming practices, buffer strips along steams, use of wetlands to improve water quality, and reduction of nitrate in river water by diversions into riparian ecosystems and the Mississippi delta (Mitsch et al., 2001). The increased runoff may also lead to problems with toxic pollutants (e.g., heavy metals and organic chemicals) if there are high levels of these chemicals in the runoff.

There is a concern that diversions carried out to restore coastal wetlands will lead to algal blooms because of the added nutrients and that they will add pollutants, which may severely affect organisms in these areas. Thus, diversions will have to be studied and managed carefully to avoid problems. On the other hand, if freshwater input decreases, it will probably lead to less accretion, lowered productivity, and saltwater intrusion. A recent study documented that reduced freshwater input to the East China Sea from the Yangtze River due to the Three Gorges Dam reduced diatom populations (Gong et al., 2006).

Changes in freshwater and sediment input to coastal ecosystems lead to complex interactions that can increase or decrease the susceptibility of coastal wetlands to climate change. As previously stated, the rate at which accretion occurs, and thus the response to SLR, is a function of the combination of the inputs of both inorganic and organic material. Organic material is mostly derived from the growth of plant roots (i.e., organic soil formation), whereas particulate inorganic material is mostly supplied in the form of sediments that come from either the sea- or freshwater sources.

There is a considerable literature showing that multiple stresses on coastal wetlands are much more detrimental than individual stressors acting alone (i.e., Mendelssohn and Morris, 2000). Coastal plants have evolved physiological, morphological, and reproductive strategies to deal with the impacts of increased and fluctuating water level. Plants are often

able to deal with moderate increases in single stressors such as increased salinity, water logging, anoxia, and toxins. But when plants are subjected to multiple stressors, their ability to adapt is greatly reduced (Mendelssohn and Morris, 2000). Freshwater input into coastal systems reduces the level of a number of stressors for example, freshwater reduces salinity, mineral sediments directly stimulate accretion, iron precipitates sulfides, and nutrients stimulate below ground productivity and thus organic soil formation (DeLaune and Pezeshki, 2003; DeLaune et al., 2003). Thus, freshwater input is a way to deal with SLR that causes both excessive flooding and salinity stress.

Enhanced above-ground production of plants from nutrient enrichment and freshwater also acts to promote trapping of sediments (Morris et al., 2002). Thus a reduction of freshwater input due to climate change reduces, in a variety of ways, the ability of coastal plants to cope with SLR. To complicate such a trend, humans have reduced freshwater flows and sediment loads to the coast worldwide (Syvitski et al., 2005). This interaction of SLR and changes in freshwater input is an example of the complex responses to both climate change and human interventions. Reduced freshwater input leads to a reduced ability of coastal wetlands to survive accelerated SLR, whereas increased freshwater input (as a result of increased river flow or because of river reintroduction) enhances survivability (DeLaune et al., 2003).

20.3.4 Coastal Fish and Fisheries

A number of investigations have demonstrated relationships between fisheries yields and the high nutrient loads, freshwater inputs, shallow depths, large areas of tidal mixing, coastal vegetated area, surface of lagoon–estuarine systems and resulting high primary productivities that are typical of estuaries, and estuarine plume ecosystems (Deegan et al., 1986; Nixon, 1988; Pauly and Christensen, 1995; Sanchez-Gil and Yañez-Arancibia, 1997; see Chapters 13 and 18). Thus, despite the small total spatial extent of estuaries (<1% of the global marine area), a much larger proportion of fisheries are derived from estuaries. In the United States, approximately 50% of fishery yields are based on estuarine or estuarine-dependent species (Gunter, 1967; McHugh, 1967; Houde and Rutherford, 1993; Vidal and Pauly, 2004).

The effects of climate change on nekton populations and fisheries are highly interactive with the factors that enhance fish and fisheries

(Chapters 13 and 18). The survival of young fish, recruitment within estuaries, and fisheries yields are related to factors such as river runoff, salinity, water temperatures during critical time periods, availability of suitable estuarine nursery habitat, precipitation, favorable wind fields, hypoxia, and sea level fluctuations. In the short term, warmer water and higher growth rates plus expansion of salt marshes inland with SLR may favor productivity of estuarine-dependent marine species. However, this enhanced productivity may be temporary because of long-term negative effects of SLR and wetland loss on fishery habitats (Kennedy, 1990; Zimmerman et al., 1991; Chesney et al., 2000; summarized in Kennedy et al., 2002).

Many of the predicted climate changes will also influence circulation patterns and transport of saltwater within coastal environments (Chapter 2). Changes in winds may alter existing circulation, especially in areas with small tidal ranges. For example, the refilling of estuaries in the northern Gulf of Mexico after strong northerly winds during a cold frontal passage is probably responsible for the transport of coastal materials and biota (e.g., saltwater, sediment, eggs, and larvae) into the estuaries (Rogers et al., 1992). Thus, changes in the intensity and frequency of frontal passages could severely alter estuarine circulation and recruitment of estuarine-dependent fish species. In addition, changes in rainfall and runoff will alter coastal and estuarine salinity gradients, thus altering circulation and long-term salinity patterns (Wiseman et al., 1986). Such changes may be sufficient to destabilize shallow coastal habitats, thereby affecting plant and animal species in these habitats.

A clearer understanding of the links between the nursery function of coastal wetlands, hydrology, and climate variation is emerging (Baltz et al., 1993; Chesney et al., 2000; Cowan et al., 2008). Interannual variation in the timing and extent of high water conditions in salt marshes may contribute to annual variation in fishery recruitment. Because many fishes make regular movements onto flooded marsh to feed, marsh access is apparently important to the growth and survival of individuals. Studies in the Mississippi delta, where astronomical tides are small, indicate that interannual variability in wind patterns influences the frequency of flooding of salt marsh habitats, and subsequently shrimp landings (Childers et al., 1990). In other coastal wetlands with larger, semidiurnal tides, marshes flood more predictably and some fishes may spend as much as one-third of their time in flooded habitats. For species that use high intertidal habitats as nurseries, variability in habitat availability

driven by climate change may have a strong influence on recruitment, particularly in the systems where tidal range is small.

In the semiarid regions, such as south Texas, the lack of freshwater and hypersalinity limit the development of emergent marshes in areas such as the Laguna Madre. Should climate change expand low rainfall regimes in areas such as the Texas coast, the area of existing intertidal marshes will diminish. This loss of nursery habitat may cause fishery yields to decline. This is supported by significant declines in shrimp and blue crab commercial yields in south Texas bays and the Laguna Madre during drought and warm winter conditions (Texas Parks and Wildlife Department, 2000). In contrast, Haas et al. (2001) predicted increased shrimp abundance in northern Gulf estuaries with increased estuarine salinity, thus highlighting the uncertainty associated with estimating the effects on fisheries of interacting variation in precipitation and river discharge, salinity, temperature, and hypoxia in climate-change scenarios.

20.4 HUMAN ACTIVITY AND COASTAL MANAGEMENT IMPLICATIONS

Increasing temperature, acceleration of SLR, changes in freshwater runoff, and increasing storm intensity are the climate forcings that will affect coastal ecosystems in many parts of the world. These forcings can interact with each other and with human impacts to either exacerbate or mitigate the effects of climate change (Day et al., 2008). For example, SLR and lower freshwater inflow lead to both increased salinity and longer flooding duration, resulting in multiple stresses on wetland plants.

Anthropogenic impacts interact with climate forcings, leading to impacts that are often more severe than either impact acting alone. For example, in deltas such as the Mississippi, Rhone, Po, Ebro, and Nile, isolation of the delta from the river (via levees and dikes), pervasive hydrologic alteration, and conversion of land to agriculture have caused high rates of coastal wetland loss (Day et al., 2007, 2012b; Stanley and Warner, 1993; Ibáñez et al., 1996; Pont et al., 2002; Vorosmarty et al., 2009). These changes have also made the deltas more vulnerable to accelerated SLR and reduced freshwater input due to climate change. In the Everglades, hydrological alterations and diversion of freshwater flows for agriculture, human consumption, and flood control have reduced freshwater input into the lower Everglades, resulting in saltwater intrusion, wetland loss, eutrophication, and habitat changes (Sklar et al., 2005; Madden, 2008; Day et al., 2012b). In addition, runoff from the agricultural area south of Lake Okechobee has caused nutrient enrichment in the upper Everglades resulting in replacement of native vegetation with *Typha* spp. In arid and semiarid watersheds, freshwater withdrawals have resulted in lowered freshwater input, and salinization of soils, as, for example, in the Indus River delta (Snedaker, 1984). These types of changes will make the effects of climate change worse, and management is needed to counter these changes. River discharge has been reduced by more than 90% for the Ebro and Nile deltas, and reduction of river input to the deltas and hydrological alterations have led to water quality problems and wetland loss. Pont et al. (2002) concluded that human impacts on the Rhone delta will worsen the impacts of climate change.

Management for climate change will necessitate working with natural systems to enhance their ability to survive climate forcings. A fundamental concept in doing this is that sustainable management should be based on system functioning (Day et al., 1997, 2000). A basic management approach is that of ecological engineering, which is defined as ''the design of sustainable ecosystems that integrate human society with its natural environment for the benefit of both'' (Mitsch and Jørgensen, 2003). This approach combines basic and applied science for the restoration, design, and construction of ecosystems. Ecological engineering relies primarily on the energies of nature, with human energy used in design and control of key processes.

For example, one management strategy to offset SLR and promote continued coastal wetland productivity is to actively utilize the resources of rivers rather than letting most freshwater, sediments, and nutrients flow directly to the sea. An example of this is the Mississippi delta where levees have led to most river water discharging directly to the Gulf. This has led to widespread wetland loss (Day et al., 2000, 2007). In an effort to solve this problem, river diversions are being used where structures allow river water and sediments to flow back into coastal wetlands (Lane et al., 1999, 2004; DeLaune and Pezeshki, 2003; DeLaune et al., 2003; Day et al., 2007, 2012a).

It is important to maintain healthy coastal ecosystems because they will better cope with climate change. This will involve careful management of freshwater, sediment, and nutrient resources and working with natural systems to adjust to climate

change. As noted earlier, diversions of freshwater can enhance the ability of coastal wetlands to survive SLR and increases in salinity. However, care must be taken to minimize the potential for eutrophication. Where possible, wetlands should be allowed to migrate inland as SLRs.

20.5 SUMMARY: A SCIENTIFIC CONSENSUS, A GLOBAL SOLUTION

As policymakers from around the world convened in Copenhagen in the fall of 2009 for the United Nations Framework Convention on Climate Change (UNFCCC), the Scientific Academies of every G8+5 nation, including the American Association for the Advancement of Science, issued a joint statement for that body to consider. The message was unequivocal:

> It is essential that world leaders agree on the emission reductions needed to combat negative consequences of anthropogenic climate change at the UNFCCC negotiations in Copenhagen in December 2009.

> Climate change is happening even faster than previously estimated; global CO_2 emissions since 2000 have been higher than even the highest predictions, Arctic Sea ice has been melting at rates much faster than predicted, and the rise in the sea level has become more rapid. Feedbacks in the climate system might lead to much more rapid climate changes. The need for urgent action to address climate change is now indisputable.

With regards to estuaries, there is much that can be done on the local level. A healthy estuarine system is resilient to environmental and anthropogenic impacts. For example, estuarine resilience to climate change can be enhanced by restoring connectivity with river and tidal energies. Tidal energy subsidizes the marsh by bringing in nutrient-rich, oxygenated water and by flushing out natural plant toxins that accumulate in the sediments. Connectivity to the river provides much needed sediments that can compensate for rising sea levels. Where possible, the removal of shoreline dikes and armoring can allow for upslope migration of estuaries as sea levels rise. Restoration and sound management can give these systems, and the organisms that thrive in them, a fighting chance in the face of climate change.

On the other hand, there is only so much accommodation and mitigation that can be accomplished at the local level. While sediment delivery and connectivity can be managed at the local scale, the overarching anthropogenic climate forcings and atmospheric greenhouse gases are a global problem. For example, as China's powerful economy continues to grow, so do its greenhouse gas emissions, which have increased 152% from 1990 to 2004 and now exceeds emissions from the United States (Leggett et al., 2008). India's greenhouse gas emissions have increased 203% from 1980 to 2000 (Stephenson, 2003).

Permanent solutions must be global solutions. The G8+5 Academies' joint statement to the UNFCCC included the following recommendations for a permanent solution to a global problem: (i) a worldwide emission reduction target of 50% from current levels by 2050; (ii) an increase in funding for research on enhancing the resiliency of natural systems to climate change; (iii) develop common, global strategies for implementing sustainable technologies; (iv) economic incentives for green technologies; and (v) pursue international cooperation on safe and secure nuclear power capacity and safe disposal of nuclear waste.

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CHAPTER TWENTY-ONE

ESTUARINE ECOLOGICAL MODELING

Enrique Reyes, Kenneth Rose, and Dubravko Justić

21.1 INTRODUCTION

Estuarine ecosystems are composed of many inter-active biotic and abiotic components (e.g., nutrients, organisms) whose functioning is not always obvious and easy to understand from observations. Estuaries are dynamic places, and their components are constantly changing. As these components and their cycles interact with each other, they create a hierarchy of dynamics in which space, time, and boundaries play critical parts. A common approach for simplifying this complexity is to develop mathematical models of these ecosystems. Models are indeed simplifications of reality and, as such, describe only the most important features and interactions in the system. Models provide a methodology that allows for data synthesis and hypothesis testing under strictly controlled conditions, which is not possible with field measurements. Models are also very useful in exploring future scenarios and can be used via hindcasting to better understand the past behavior of the system.

Research and development in estuarine modeling have paralleled the developments in estuarine physics, chemistry, and biology. Holistic perspectives of estuarine ecosystems in the 1970s required the construction of conceptual and mathematical models that tested current knowledge and directed future research. Estuarine modeling is a systematic approach to addressing environmental problems and for directing research. The power of modeling is that it requires one to propose a mathematical representation of the ecosystem and thus tests our knowledge and understanding of the system. As the holistic approach gained popularity (Odum, 1960), estuarine systems became probing grounds for modeling efforts. Among the first holistic-based modeling studies were those of Teal (1962) working in salt marshes, Pomeroy et al. (1972) examining phosphorus flux in estuaries, and Nixon and Oviatt (1973) modeling *Spartina*. Wiegert et al. (1975) and Ulanowicz et al. (1975) combined an empirical microcosm phytoplankton experiment with a simulation model. Dame (1979) is an excellent source of information on these early modeling efforts. Owing to the developments in computer technology, the use of simulation models has grown explosively over the past two decades. For example, in their review of estuarine biogeochemistry models, Jorgensen and Bendoricchio (2001) listed more than 50 different models. Most of these models were concerned with specific problems, such as predicting the effects of eutrophication on water quality and simulating the cycling and fate of toxic compounds in the ecosystem.

21.2 CLASSES OF MODELS

Models can be generally divided into conceptual (qualitative, diagrammatic, textual) and mathematical (quantitative). Conceptual models often use flow

diagrams (boxes and arrows showing energy and mass transfers among boxes) to illustrate the relationships among model components, and lately, conceptual models have become a very popular approach to evaluate and justify the decisions as to which projects to undertake in large ecosystem restoration efforts (Twilley, 2004; Ogden et al., 2005; Rudnick et al., 2005).

Mathematical models typically include one or many equations that are used in model computations. Mathematical models can be further subdivided into statistical and mechanistic models.

Statistical models are built primarily from empirical data. They are purely descriptive, and the relationships among variables represented in the model are not necessarily causal. Examples of statistical models include simple models of primary productivity (Cole and Cloern, 1985; Hume and Herdendorf, 1993; Howell et al., 2005), population dynamics of organisms (Tumbiolo and Downing, 1994; Goss-custard et al., 1995), and even highly sophisticated watershed and ecological models (Corbett et al., 1997; Thompson et al., 2000; Paul et al., 2002).

Mechanistic models are process-based models that are built on how we believe the ecosystem functions. These models often include descriptions of various physical, chemical, and biological processes and require extensive calibration and testing. Mechanistic models try to go beyond statistical models and include cause-and-effect relationships. Examples of mechanistic models include surface and subsurface water flows (Wynn and Liehr, 2001; Rousseau et al., 2004), biogeochemical cycles (Potter, 1997; Merrill and Benning, 2006), and population dynamics (Wortmann et al., 1997; Baird et al., 2003).

While it is convenient to classify models, most models are a mix of statistical relationships and process representations. Some believe that statistical models, which are simpler and more directly rooted in data, are better for predicting, while mechanistic models are better for increasing our understanding of the ecosystem. This debate over how simple or complex models should be continues to this day.

Estuarine models are typically constructed using a series of highly interrelated steps (Fig. 21.1). These steps are often repeated and, in practice, models are developed by going through these steps several to many times.

21.2.1 Conceptualization

The first step in model construction is to describe the prediction variable of primary interest and the major components that we believe affect this variable. The main questions we use to conceptualize the model

are: How do we think the system of interest works? What are the components and processes that greatly influence the dynamics of the system? Very important to the conceptualization step is a clear statement of the question or hypothesis of interest. Once the question of interest can be stated, one can begin to decide what is important to include in the model. Specific aspects of the conceptualization step are deciding on the currency of the model (the units in which the model calculations are computed, e.g., mass or energy), the variable or variables of interest (called state variables) one wants to predict over time or in space, the major processes or components that need to be included in order to sufficiently predict how the state variables will change over time and space, and what environmental variables regulate these processes.

21.2.2 Formalization

The next step after conceptualization is to formalize the model by adding more details to the conceptualized model. What exactly are the state variables, processes, and environmental variables (also called forcing functions) needed to sufficiently describe the conceptualized model? Just as important is what aspects of the ecosystem can be ignored and not included in the model. Remember a model is, by definition, a simplification of the real ecosystem; thus, things we know operate in the real ecosystem must be left out or greatly simplified in a model. An important aspect of the formalization step is to list the assumptions that need to be made as a result of the simplifications that underlie the model. Formalization involves defining the spatial scale and boundaries of the model and the temporal scales of the model. Specification of the spatial scale involves deciding how many spatial boxes will be represented and the dimensions of each of these boxes, what area in total will be covered by the spatial boxes (e.g., entire estuary or the near-shore zone), and how to deal with the boundaries in terms of how the modeled area is linked to areas just outside of the modeled area. For example, do materials or organisms enter and exit the modeled area, and if so, what is their rate of exchange. Specification of the temporal scales involves deciding on the time step of the model (how often the values of the state variables are updated) and how long model simulations will be. The result of conceptualization and formalization is often a detailed diagram. This type of diagram is critical to determine which components are important to include in the model and how they relate to each other, in order to be able to answer the question or hypothesis of interest. Sometimes the questions of interest evolve
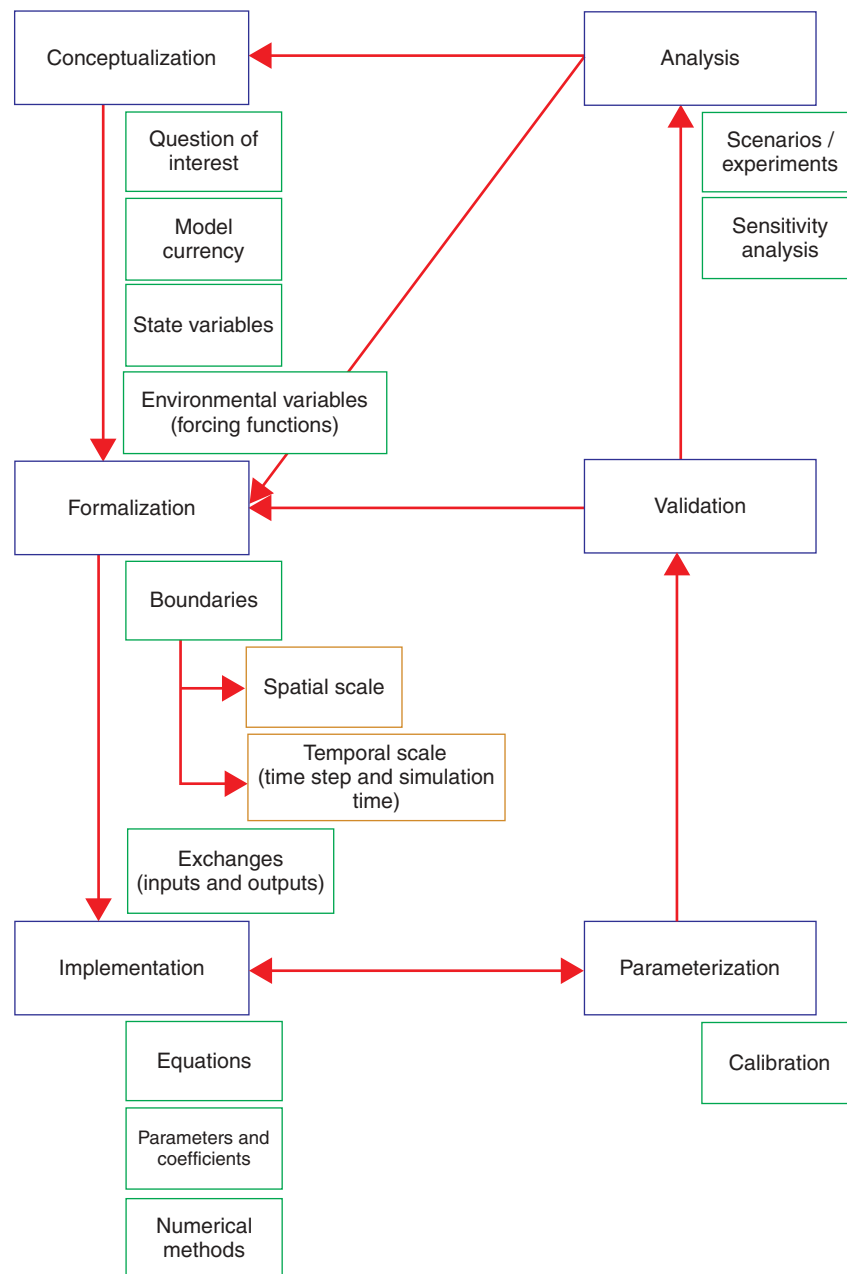
FIGURE 21.1 Conceptual diagram showing the major steps in the construction of an ecological model.

during the development of the model. One must always ensure that the conceptualized and formalized model remains appropriate for the current question of interest.

21.2.3 Implementation

A conceptualized and formalized model is ready to be expressed in mathematical terms, which we call the implementation step. The implementation step involves translating words and diagrams into model equations. The dependence of the state variables on processes (and thus on environmental variables that affect the processes), and on each other, is expressed as equations. Several types of mathematics can be used to express these equations, which are often grounded in calculus. The commonly used mathematics are differential equations and difference equations. Usually, there is an equation that describes the rate of change of each state variable. With multiple state variables, one obtains a system of equations in

which the equation for a state variable may include terms that involve the values of other state variables. The specific types of mathematics used then determine the numerical techniques needed to solve these equations, and to thereby obtain values of the state variables over time and, if appropriate, over space. While the details of the mathematics and the solution methods are often not described, it is very important to be sure that one is obtaining the correct solution to the model equations. As part of the implementation step, model parameters or coefficients that determine the rates of the processes, and thus the rates of change of the state variables, are carefully defined. Computer-related questions are also dealt with in the implementation step, such as whether off-the-shelf computer software can be used to solve the equations or which programming language should be used to develop a customized code that solves the model equations.

21.2.4 Parameterization

While values for some parameters and forcing functions can be estimated with great accuracy and precision, some or many parameters are only known approximately. Some processes, and the associated parameters, can be specified from first principles, such as the number of calories in a gram of respired oxygen. Many processes use measurable parameters, but these parameters either have not been measured yet or have reported values that have been determined for only a few conditions (e.g., 1 year in one place in the estuary), in the laboratory, or only in other ecosystems or for other species. Rarely are estuarine models developed for which all parameters are known with great confidence. An important aspect of the parameterization step is model calibration; the determination of values of imperfectly known model parameters. Calibration can involve simply making educated guesses at parameter values, repeated adjustment of parameter values until the model behaves reasonably, or statistical-based calibration approaches that involve algorithms for searching for the set of parameter values that make the model predictions of state variables as close as possible to the observed values of the state variables. The decision of how to calibrate a model depends on the mathematics and complexity of the model itself, the purpose of the model, and the quality and quantity of the available data.

21.2.5 Validation

Confidence in models often depends on how well a model predicts values of state variables for data that was not used to construct the model (i.e., measurements of state variables not used in the previous steps). This is commonly known as the independent test of a model. It is not always possible to rigorously test a model against independent data. But a good validation demonstrates the degree to which model predictions can be generalized and applied beyond the conditions underlying the calibration (parameterization) step. While having a model accurately predict the values of state variables for new conditions is reassuring, a very useful result of model validation is also having the model do poorly and thereby help define the limits of the model. Model validation almost always also raises questions about the quality and quantity of the data. As one models long-lived animals such as fish, the data are rarely sufficient for rigorous model validation and sometimes validation results in the question is the model wrong or are the data not representative of general conditions?

21.2.6 Analysis

A calibrated and validated model is then used to address the original question or hypothesis of interest. Model analysis can be simply several simulations under a variety of conditions or a specific set of simulations performed as if an experiment was being performed. Of course, this experiment is in the virtual world. This has the advantage of being able to control everything in the simulated ecosystem so that the effects of certain factors can be isolated, and the effects of simultaneous variation in multiple factors can also be cleanly examined. However, the results are only as good as the model is realistic. The analysis step often also involves sensitivity analysis, which varies model parameters in a systematic way to determine which parameter has the greatest influence on model predictions and to provide information on the range of parameter values under which the model can still generate realistic outcomes. Sensitivity analysis is typically done by varying each parameter in the model by a small, fixed amount. The change in model predictions of state variables between the original simulation and with a parameter increased by say 10% is an index of the sensitivity of the model to that parameter. It is observed that 10% changes in some parameters will cause large changes in model predictions, while similar changes in other parameters will have little effect. Complex models generate multiple prediction variables, and the importance of parameters can vary among the prediction variables. Uncertainty analysis is an extension of sensitivity analysis that uses more sophisticated ways to change parameter values, both

singly and together, and changes parameter values by realistic amounts that reflect how the parameter varies in nature. The results of model experiments and sensitivity and uncertainty analysis, taken together, are used to answer the original question or hypothesis of interest.

The next section consists of three modeling examples that illustrate how models have been used to address important questions about estuaries and their responses to change. In all three examples, models were used because other methods (such as data collection) would be impossible, difficult, or expensive. Each example involved multiple passes through the model construction steps outlined above. All these models to this day are still undergoing modifications, which are hopefully improvements, as more data and information become available and the questions of interest continue to evolve and new questions are posed.

21.3 CASE STUDY: RESPONSES OF THE GULF OF MEXICO HYPOXIA TO VARIATIONS IN CLIMATE AND ANTHROPOGENIC NUTRIENT LOADING

Large-scale hypoxia (< 2 mg O_2/l) in the northern part of Gulf of Mexico (Fig. 21.2), recently exceeded an area of 20,000 km^2 (Rabalais et al., 2002), and this hypoxic area overlaps with the habitat and fishing grounds of commercially important fish and shrimp species. Hypoxia develops as a synergistic product of the high stability of the water column and high surface primary productivity. High stability prevents mixing of oxygen-rich surface waters with the isolated bottom layer, and high surface productivity results in high carbon flux to the bottom layer where decomposition results in the depletion of oxygen (Rabalais et al., 1996). Hypoxia in the northern part of Gulf of Mexico typically occurs from March through October in the bottom layer waters located below the pycnocline and extends between 5 and 60 km offshore (Rabalais and Turner, 2001). Retrospective analyses (Turner, and Rabalais 1994; Sen_Gupta et al., 1996) and model simulations (Justić et al., 2002) have suggested that the Gulf's hypoxia has intensified during the past five decades as a result of increased nitrogen inputs by the Mississippi River and a more balanced mix of nutrients in the river water (Turner and Rabalais, 1991; Justić et al., 2003).

As the northern part of Gulf of Mexico supports important US fisheries, hypoxia has received considerable scientific and public attention. In 2001, the Mississippi River/Gulf of Mexico Watershed Nutrient Task Force set a goal to reduce the 5-year running average of the Gulf's hypoxic zone to less than 5000 km^2 by the year 2015 (Rabalais et al., 2002). The proposed action plan suggested that a 30% decrease in the Mississippi River nitrogen load to the Gulf would be needed to reach this goal and that the plan's implementation should be based on voluntary, incentive-based strategies implemented in the large, Mississippi River watershed that ultimately feeds into the Gulf of Mexico.

While the link between the anthropogenic nutrient inputs coming from the upstream watershed and hypoxia was addressed in the proposed action plan, it was also recognized that the development of hypoxia in the northern part of Gulf of Mexico is highly sensitive to interannual variability in the Mississippi River discharge (Fig. 21.2). For example, during the drought of 1988 (a 52-year low discharge record of the Mississippi River), the aerial extent of midsummer hypoxia was minimal. In contrast, during the flood of 1993 (a 62-year maximum discharge for August and September) the hypoxic zone was twice the averaged area for 1985 to 1990.

To address the question of the effect of interannual variability in Mississippi River discharge on the hypoxic area, a mathematical model was constructed to simulate the monthly responses of the hypoxia in Gulf of Mexico to variations in climate and anthropogenic nutrient loading. The model made use of the data collected for 45 years between 1955 and 2000. Once calibrated, the model was used to simulate the effects of six hypothetical future scenarios on the frequency and area of the hypoxic zone. The future scenarios were based on observed and projected changes in the Mississippi River discharge, nitrate concentrations in Mississippi River water, and ambient water temperatures in the northern part of Gulf of Mexico. One scenario corresponded to a proposed management measure and examined what would happen to hypoxia with a 30% decrease in the nitrogen flux into the Gulf from the Mississippi River.

21.3.1 Approach to Modeling

A simple two-box model was constructed (Justić et al., 1996, 2002) that allowed for different dynamics in the surface layer and in the bottom layer. The surface layer was defined as above the pycnocline (0 to about 10 m deep) and the bottom layer as below the pycnocline (depths of 10 to about 20 m). The model assumed
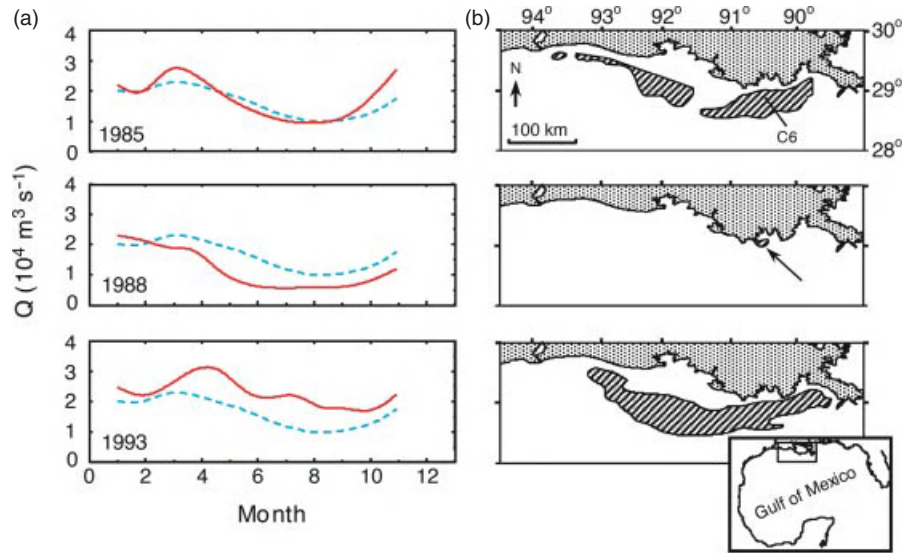
FIGURE 21.2 The Mississippi River discharges (Q, a) and corresponding areas of summertime bottom hypoxia (b) in the northern part of Gulf of Mexico during 1985, 1988, and 1993. The solid line represents the mean monthly discharge for a given year, and the dashed line is the mean monthly discharge for the 1985–1993 period. The shaded areas represent the distributions of bottom waters with dissolved oxygen concentration below 2 mg O_2/l. Note that during 1988, hypoxia was observed only at one location off the Louisiana coast. The reference station C6 is indicated in the upper panel of (b) *Source*: Reprinted from Justić et al., 2003, with permission from Elsevier.

uniform properties within the surface and bottom layers. In the model, the oxygen concentration in the surface layer changed as a result of biological oxygen production and consumption, oxygen transport in the horizontal and vertical directions, and exchange with the atmosphere. In the center of the hypoxic zone, horizontal oxygen transport due to advection and diffusion is small compared to vertical oxygen transport (Justić et al., 1996). Thus, the equation for the state variable of the daily oxygen concentration in the surface layer (O_{ts}, g O_2/m^2) was

$$\frac{\partial O_{ts}}{\partial t} = -F_{Ot} - D_O + NP \qquad (21.1)$$

where t is the time (day), F_{Ot} is the total air–sea oxygen flux (g O_2/m^2/day), D_O is the diffusive oxygen flux through the pycnocline (g O_2/m^2/day), and NP is the net primary productivity expressed in terms of oxygen equivalents (g O_2/m^2/day). The net productivity of the surface layer (NP; g C/m^2/day) was computed at each time step from a time-delayed regression model ($r^2 = 0.73$; $p < 0.001$; Justić et al., 1996)

$$NP_t = -0.34 + 3.93x10^{-7}(N-NO_3)_{t-1} \qquad (21.2)$$

where $N - NO_3$ is the nitrate flux of the Mississippi River (10^6 kg/day) and subscripts t and $t-1$ denote

the current and the preceding month, respectively. Conversion of carbon to oxygen equivalents, so that Eq. 21.1 is dimensionally correct, was carried out using a ratio of 3.47 by weight (mol C/mol O_2 = 106: 138; Redfield et al., 1963).

Owing to the high turbidity of the continental shelf waters near the Mississippi River, biological oxygen production below a water depth of 10 m is low (Lohrens et al., 1990) and may be considered an insignificant term when compared to vertical oxygen transport. Thus, the differential equation for the state variable of oxygen concentration in the bottom layer (O_{tb}, g O_2/m^2) included only two terms: oxygen uptake due to benthic and water column respiration (R) and oxygen resupply from the upper water column via turbulent diffusion (D_O)

$$\frac{\partial O_{tb}}{\partial t} = -R + D_O \qquad (21.3)$$

The respiration rate (R; g O_2/m^2/day) in the bottom layer at any given time t may be expressed in terms of the net productivity rate NP(t) at some earlier time t_0, so that

$$R(t) = k(t) \int_{-\infty}^{t} a\, NP(t_0) \exp\left[\int_{-t_0}^{t} k(t_1)dt_1\right] dt_0 \qquad (21.4)$$

where the proportionality constant α describes the fraction of NP that reaches the lower water column. Equation 21.4 used net productivity as a surrogate for excess carbon in the surface layer that is available for export to the bottom layer. Accordingly, the equation for the rate of change of the state variable of organic carbon in the sediments (C_s, g C/m^2) may be written as:

$$\frac{\partial C_s}{\partial t} = S_f(t) - R(t) - E_c \qquad (21.5)$$

where S_f is the instantaneous vertical carbon flux, resulting from the sedimentation of organic material from the surface layer (g C/m^2/day), $R(t)$ is the respiration rate in the bottom layer, expressed in terms of carbon equivalents (g C/m^2/day), and E_c (g C/m^2/day) is the loss of sedimentary carbon because of the processes of resuspension and export.

Equations 21.1, 21.3, and 21.5 represent a system of coupled, nonlinear differential equations. In simulation experiments, the equations were solved using the Runge–Kutta integration method of the fourth order and an integration step of 0.01 months (0.3 days).

21.3.2 Model calibration

The model was calibrated using data from 1985 to 1993 for the Mississippi River and the northern part of Gulf of Mexico. The 1985–1993 period included three average hydrologic years (1985, 1986, and 1989), a record flood year (1993, a 62-year record high discharge), two years with above average discharge (1990 and 1991), three years with below average discharge (1987, 1988, and 1992), and a record drought year (1988, a 52-yr record low discharge). Given the time span of the data, the 1985–1993 data subset was well suited for model calibration because the data contained a wide variety of river discharge conditions. Calibration results for surface layer and bottom layer oxygen concentrations (Fig. 21.3) showed that the model agreed very well with the observed values.

21.3.3 Model Results

The future scenarios that were investigated with the calibrated model (Table 21.1) were based on projected changes in the Mississippi River discharge, Mississippi River nitrate flux into the Gulf and ambient water temperatures in the northern part of the Gulf of Mexico. Model predictions under the future scenarios were compared to the baseline simulation results, in which the model was forced by the observed time series of temperature, river fresh water discharge,
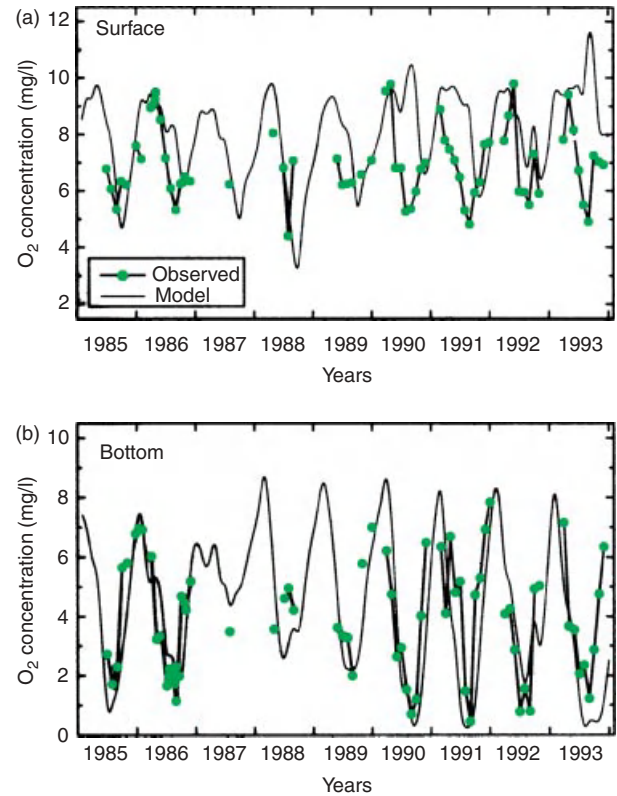
FIGURE 21.3 Observed and predicted monthly averages of (a) surface (0–10 m) and (b) bottom (10–20 m) oxygen concentrations at station C6 for the period June 1985–November 1993. *Source*: Reprinted from Justić et al., 2002, with permission from Elsevier.

and nitrate flux for the 45-year period from 1955 to 2000.

Model predictions under baseline conditions identified the mid-1970s as the start of recurring hypoxia in the bottom layer and predicted a total of 19 years with hypoxia between 1955 and 2000 (Fig. 21.4). These results are in good agreement with the timing of first reports documenting hypoxia in the northern part of Gulf of Mexico (Rabalais and Turner, 2001) and are additionally supported by the retrospective analyses of sedimentary records (Turner and Rabalais, 1994).

For a future scenario with a 30% decrease in the average Mississippi River discharge (Table 21.1, Scenario 1), the model predicted 8 years with hypoxia, which is a 58% decrease in frequency relative to the baseline results. On using riverine nitrogen inputs characteristic of 1955–1967 (Scenario 2), no data on hypoxia were obtained. For a scenario with 20% increase in the average Mississippi River discharge (Scenario 3), the model predicted a 37% increase in frequency of hypoxia. A 4 °C warmer northern part

TABLE 21.1 Simulated changes in the average oxygen concentration of the bottom layer in the core of the Gulf's hypoxic zone for a number of climatic and nitrogen loading scenarios

Scenario		Number of Years with Hypoxia	Percentage Change Relative to Baseline
Baseline	1955–2000 conditions	19	—
1	30% reduction in river discharge	8	−58
2	Nitrate concentrations characteristic of 1955–1967	0	−100
3	20% increase in river discharge	26	+37
4	4 °C warmer Gulf waters	25	+32
5	20% increase in river discharge and 4 °C warmer Gulf waters	31	+63
6	30% reduction in nitrate concentration	12	−37

The baseline model was forced using time series of observed monthly values of the Mississippi River discharge, and nitrate concentration $(N - NO_3)$ over a 45-year period from 1955–2000. The investigated model scenarios are based on the available projections of climate, Mississippi River flows, and temperatures in the northern part of Gulf of Mexico, and proposed nutrient management goals. Hypoxia is defined as water with DO less than 2 mg O_2/l.
Source: Adapted from Justić et al., 2003.
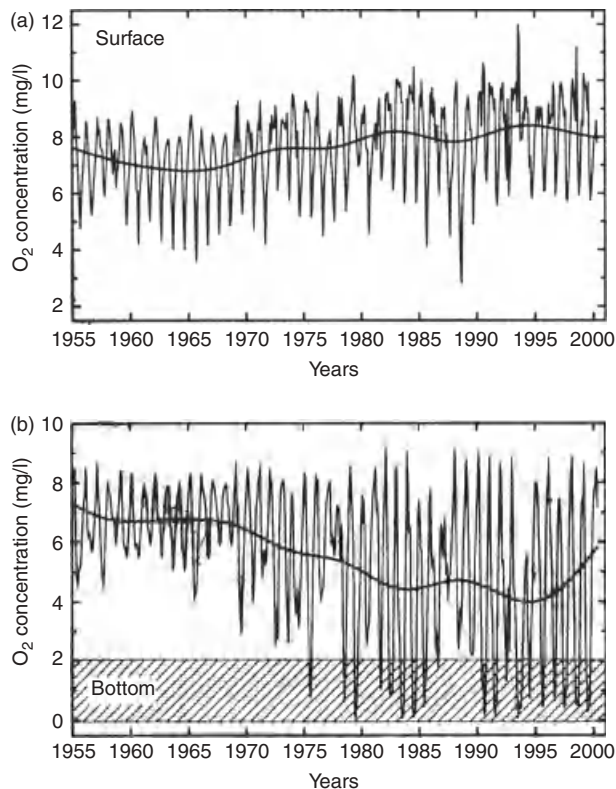
FIGURE 21.4 Simulated changes in the average (a) surface (0–10 m) and (b) bottom (10–20 m) oxygen concentrations at station C6 for the period January 1955 to May 2000. Shaded area in the lower chart denotes hypoxic conditions (<2 mg O_2/l) in bottom waters. *Source*: Reprinted from Justić et al., 2002, with permission from Elsevier.

of Gulf of Mexico (Scenario 4) would result in a 32% increase in the frequency of hypoxia over the baseline, and the combination of a 4 °C warmer Gulf and a 20% increase in the average Mississippi River discharge (Scenario 5) would result in 31 years with hypoxia or a 63% increase in the frequency over the baseline. While a 30% decrease in the Mississippi River nitrate concentrations (Scenario 6) would result in a 37% decrease in the frequency of hypoxia, this decrease in hypoxia is offset if a 20% increase in the Mississippi River discharge occurred at the same time.

21.3.4 Lessons Learned

Hypoxia in the Gulf of Mexico is highly sensitive to variations in fresh water discharge, riverine nitrate flux, and the ambient water temperatures in the Gulf. Depending on the assumptions about future climate change, both major increases and decreases in the frequency of hypoxia are possible (Table 21.1). It is difficult to predict changes in the aerial extent of hypoxia based on model projections for a single station within the core of the hypoxic zone (C6; Fig. 21.2). In this respect, it was not possible to determine whether a 30% decrease in nitrate flux would reduce the average aerial extent of hypoxia below 5000 km^2, as suggested by the Mississippi River Watershed/Gulf of Mexico Hypoxia Task Force (Rabalais et al., 2002). Nevertheless, model simulations indicated that if potential climatic variations are taken into account, a 30% decrease in the nitrogen flux of the Mississippi River may not be sufficient to accomplish the proposed hypoxia management goal. For instance, a 20% increase in the Mississippi River discharge, projected under some climate change scenarios, would completely offset a decrease in the frequency of hypoxia resulting from a 30% decrease in the anthropogenic nitrogen flux.

21.4 CASE STUDY: EFFECTS OF MARSH HABITAT ON BROWN SHRIMP PRODUCTION

Many shellfish and fish use the marshes in estuaries as nursery areas (Minello, 1999). For example, brown shrimp (*Farfantepenaeus aztecus*) spawn offshore in the ocean, and very young shrimp then move shoreward until they reach estuaries and settle to the bottom between February and May when they are about 15 mm in length. While in the bays and marshes of the estuary, the young shrimp grow rapidly in size, and on reaching about 70 mm in length in the fall, they leave the estuary and return to the ocean. Sampling with nets has shown that the young shrimp congregate in the edge habitat where the marsh meets the water (Rozas et al., 2000). Harvesting of shrimp in the offshore waters is a very important fishery in the Gulf of Mexico.

In many areas, including the Gulf of Mexico, marshes are disappearing because of rising water due to sea level rise, man's prevention of the natural flooding of rivers that used to bring sediments to the marshes and build them up, and natural processes such as subsidence (compaction of the soils under the marsh) (Boesch et al., 1984). There was general concern about how the continued loss of marshes might affect the shrimp during their important nursery period in the estuaries. It was difficult to determine this from field sampling only because comparison of shrimp growth and mortality among marshes could be affected by other differences between the marshes than just their degree of degradation. Thus, Haas et al. (2004) developed a simulation model of the shrimp during their time in the marshes with the purpose of predicting how degradation of the marshes, with all else equal, would affect the growth and mortality of young brown shrimp. Their results could also be viewed in the reverse direction as how shrimp growth and mortality might be expected to respond if already degraded marshes were restored.

21.4.1 Approach to Modeling

Haas et al. (2004) constructed an individual-based model of brown shrimp in which each modeled shrimp moved around in a square grid of spatial cells. The model was run for 245 days (January 1 through September 1), with state variables being updated every 6 h. The state variables were the size (length in millimeters), status (dead or alive), and cell location of each individual shrimp. By summing over all live shrimp, Haas et al. (2004) obtained predictions of total shrimp; they also kept track of the numbers of shrimp surviving to 70 mm when they leave the estuary and return to the ocean. The processes of growth affected the size of each shrimp, mortality determined the status of each shrimp, and movement determined the location of each shrimp. The environmental driving variables were water temperature, which affected growth, and flooding, which determined whether cells in the grid had water on them and were therefore accessible to the shrimp. Very young shrimp (about 15 mm in length) were added to the simulated population every week between January and May according to field data, and were started by randomly placing them in cells that had water.

Aerial photographs of actual marshes were used to designate each of the 10,000 cells in the 100×100 grid either as vegetated or open water. Each cell had 1 m sides. Four particular photographs were selected that provided a nice contrast in the health of the marshes (Fig. 21.5). Two of the habitat maps had about 50% water cells, but one had a large cluster of vegetated cells (low edge), and the other had the same amount of vegetated cells but in many smaller clusters (i.e., was more fragmented and therefore had more edge). The other two habitat maps had similarly highly clustered or fragmented vegetative cells, but with less vegetative cells in total (closer to 30%, rather than 50%, of the map). One could view the degradation of a marsh as starting with the one with low edge with high vegetation and then going clockwise around the maps. The most degraded marsh would be the low edge with low vegetation map.

Water temperature was updated each day from a function fitted to field data, and all cells were assumed to have the same water temperature. Flooding was represented in a more complicated way. Each cell could be in one of four stages (low tide, rising, high tide, falling). A function was fit to the field data based on the probability of flooding occurring on a day. Each day in the model, it was randomly determined whether flooding occurred, and then the stages were updated for the next four 6-h time steps until the next day when the process was repeated. If flooding occurred on a day, then the stages were changed for the next four 6-h time steps to mimic rising water (low went to rising, rising to high, falling to high). If flooding did not occur, then the stages were changed to mimic falling water levels (high to falling, falling and rising to low). Vegetated cells more than one cell away from permanently watered cells were accessible to the shrimp only when they were in the high tide stage, whereas vegetated cells at the edge where they
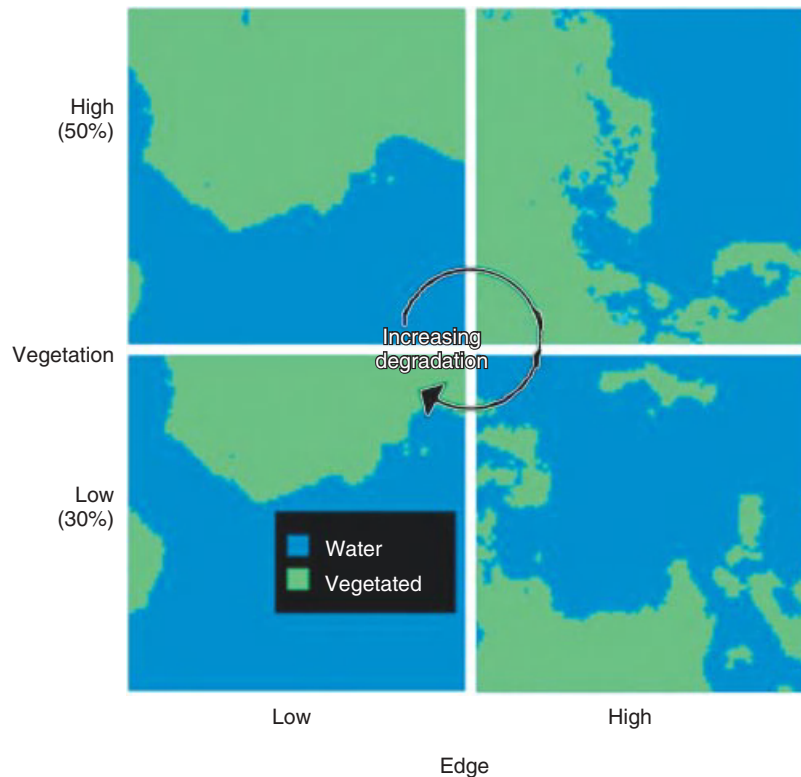
FIGURE 21.5 The four spatial maps of vegetated and water cells in the 100×100 grids used for simulating individual brown shrimp growth, mortality, and movement. The two maps on the top row had similar total amount of vegetated cells (50%). The left-side map had this arranged in large clumps and thus low edge, while the right-side map has smaller clumps and thus higher edge. The bottom row had few vegetated cells (about 30% of the map) and also arranged such that the left-side map had low edge and the right-side map had high edge. The four maps can be thought of as showing a progression of degradation as one goes clockwise starting at the top left map.

meet water cells were accessible when the shrimp were in the rising, falling, and high tide stages.

Growth rate was computed every 6 h for each shrimp, and the new length was computed. Growth started at 0.25 mm/6 h for all shrimp, then adjusted depending on the number of other shrimp that were in the cell with them (more shrimp lowered the growth rate because of other shrimp eating the food) and the water temperature in the cell (faster growth with warmer water until it was too warm), and was faster in vegetated cells than in open water cells.

Mortality rate every 6 h depended on the size of the individual shrimp (larger shrimp have lower rates) and the number of cells the shrimp moved (shrimp are more vulnerable to being eaten when moving), and it was lower in vegetated cells because of protection from predators. Every 6 h, the different sources of mortality were computed and combined into a single total mortality rate for each shrimp. A random number between 0 and 1 was generated and compared to the probability of dying based on the total mortality rate. Dead shrimp were removed

from the simulation and were no longer evaluated in future time steps for growth or movement.

Movement is very tricky to model because we are just now learning about the details of fine-scale movement of animals. Measurements are now being made using electronic tags and other high tech methods. So Haas et al. (2004) decided to use a series of rules to move individual shrimp around the grid of cells every 6 h and then compared the spatial patterns of their distributions to field data. Of course, just because the predicted and observed patterns agree does not mean that the rules are correct. There may be several sets of rules that result in similar spatial patterns. Without going into the details, Haas et al. (2004) modeled the process of movement by allowing each shrimp to look at cells neighboring its present location and try to go to the cell that would give it the fastest growth rate. Larger shrimp examined larger neighborhoods, and shrimp in water cells also looked at larger neighborhoods than those in vegetated cells. Only cells that had water were included as possible destinations. This meant that candidate cells to move

to were: vegetated cells at high tide; edge vegetated cells at low, rising, or high tide; and water cells all of the time. The movement rules were programmed in the computer code as a complicated series of IF-THEN conditional statements, with all ending up in a shrimp either staying in its present cell or moving to a neighboring cell.

The model was coded in the FORTRAN programming language, and simulations were performed on a fast personal computer. The mathematics of the model is a series of difference equations, with an equation each for the length of a shrimp, the status (dead or alive) of a shrimp, and the current cell location of a shrimp. With difference equations, the solution technique is simply to go through each shrimp every 6 h and update the equations based on the values from the previous time step. This sounds easy, but can be tricky, because the order in which the state variables are updated can affect the predictions. The computer code was about 3000 lines. Each simulation involved introducing a total of 100,000 shrimps (spread over January through May). These shrimp were added weekly, and once in the model, were evaluated every 6 h for growth, mortality, and movement. The tidal stage of each cell was updated every 6 h based on whether flooding occurred or not, which was determined once a day.

21.4.2 Model Calibration

The model was calibrated by mostly tweaking the movement rules until realistic behavior was obtained, especially whether the predicted spatial distribution of shrimp in the summer looked like the pattern inferred from field data. Haas et al. (2004) adjusted the sizes of the neighborhoods searched and other aspects of the movement, as well as the mortality rates, until reasonable densities (numbers of shrimp per square meters) were obtained over time, and shrimp seemed to be congregating in edge habitat, in agreement with the field data. They used the high edge with high vegetation map for calibration because most of the field data was from sampling on this type of marsh. There was not much data available for a true validation using independent data.

Introducing 100,000 shrimp, with the simulated growth, mortality, and movement, resulted in peak densities in April of about 20 shrimp/m^2 at high tide in edge cells, and averaged densities in vegetated cells about eight times those in open water cells and about three times higher in edge cells compared to interior marsh cells. Haas et al. (2004) examined the model output looking for patterns in shrimp densities by tide stage and season in the different habitats (on the marsh, in the edge, and in open water). These values and patterns matched field data quite well.

21.4.3 Model Results

Once calibrated, Haas et al. (2004) used the model to simulate the number of shrimp reaching 70 mm on the four maps. All other factors, such as temperature, pattern of weekly introduction of newly arrived shrimp, and flooding patterns, were maintained the same; the only difference was the maps.

Predicted percentage of the 100,000 initial shrimp that survived to reach 70 mm was higher in maps with high edge. Predicted survival was higher in maps with high edge (28% in low vegetation and 31% in high vegetation) compared to the two maps with low edge (23% in low vegetation and 24% in high vegetation). Sleuthing in the model results showed that the higher survival was due to shrimp spending more time in the edge cells, where they grew faster and had lower mortality rates.

Haas et al. (2004) went on to perform many more simulations using the model and the four habitat maps. They reran the simulations by introducing 300,000 and 600,000 individuals to determine the effect of crowding on growth, survival, and movement. They also reran the simulations with alternative rules about movement, such as making the neighborhood searched smaller and larger.

21.4.4 Lessons Learned

The Haas et al. (2004) analysis provided valuable information on the role of edge habitat and marsh loss on shrimp survival and growth. They were somewhat surprised that the differences in survival to 70 mm among the four maps were not larger. If the model is realistic, the shrimp, at least in the virtual world of this model, are good at finding the edge habitat, even on maps with relatively low edge and low vegetation. Haas et al. (2004) went on to illustrate that even this seemingly small change in survival to 70 mm can be biologically important. They performed some simple calculations that extrapolated the model results to the entire coast of Louisiana and showed that the difference between the lowest and highest survival, if applied to the entire coast, would be a difference of about 36 million lb, or about the annual catch of shrimp in the Gulf of Mexico. The model of Haas et al. (2004) also showed that measurements on the movement of shrimp on small scales (meters and hours) would be a worthwhile area to pursue. Putting tags and other devices on individual shrimp to record

their movement is not quite possible yet, but will likely be in the next few years as the technology gets smaller. We need to confirm or reject the fact that the shrimp can find edge habitat as well as suggested by the movement rules encoded in the model. Finally, the analysis of Haas et al. (2004) is a good example of the power of the individual-based approach in estuarine modeling. Following thousands of individuals, while computationally complicated, made putting in the biology about movement and how shrimp are affected by the fine-scale spatial arrangement of the marsh cells very easy.

21.5 MODELING ESTUARINE WATERSHED DYNAMICS

Coastal areas in the Mississippi delta region are changing at unprecedented rates, with major displacement of fresh water vegetation by more salinity-tolerant communities and substantial loss of wetland resulting in conversion of vegetated areas into open water (Coleman et al., 1998; Day et al., 2000; Tornqvist et al., 2002). Within coastal Louisiana, wetland loss rates have ranged from 73 to 102 km^2/year (Gagliano et al., 1981). These high rates of coastal land loss have prompted much research over the past half century on the root causes of this land loss (Deegan et al., 1982; Penland and Ramsey, 1990; Britsch and Dunbar, 1993) and much debate of management approaches on how to address this problem (Templet and Meyer-Ardent, 1988). In large watersheds, interactions among factors such as sea level rise, subsidence, climate variability, accretion, wetland elevation, wetland health and productivity, and water levels are most important in determining the long-term sustainability of coastal wetlands. Human impacts, such as the leveeing of the Mississippi River, creating impoundments, and constructing canals have altered the hydrology, salinity, and sediment dynamics of coastal wetlands. Among the most favored management options are river diversions that would restore the riverine inputs to more natural conditions in order to preserve and enhance areas of deltaic wetlands (Pezeshki and DeLaune, 1996; Coleman et al., 1998; Martin et al., 2002).

To help in assessing the effects of river diversions on wetland persistence, a spatially explicit model of coastal wetlands was developed and applied to the Caernarvon diversion project. The Caernarvon fresh water diversion outlet is among the seven diversions currently in operation in the lower part of Mississippi River. The Caernarvon diversion structure dominates
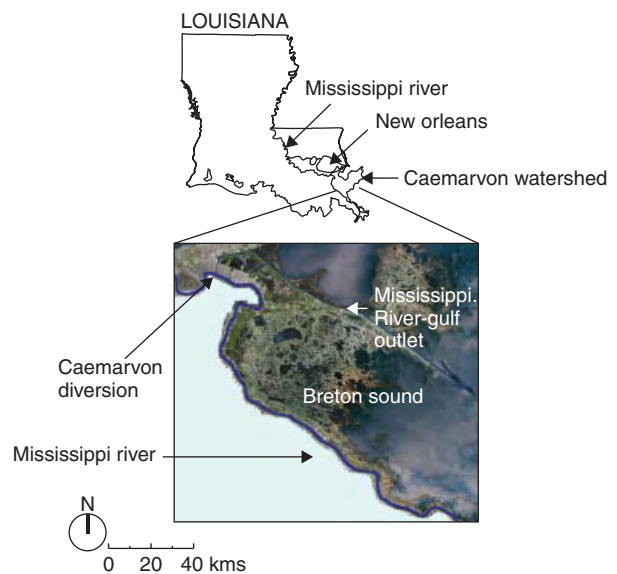
FIGURE 21.6 Location of the Caernarvon basin where the watershed model was applied to simulate long-term plant community changes under different fresh water input scenarios.

the fresh water inputs into the nearby watershed. The structure was completed in 1991 and has had a discharge averaging 21 m^3/s. In addition to the practical application of the model to a real-life river diversion, the model was also used to test our knowledge about how estuarine wetlands function over long term (Day et al., 1997). The most important feature of this watershed model was that it simulated a broad geographic area (Fig. 21.6) and attempted to project how river pulsing of water would affect the plant community in this region for 50 years into the future.

21.5.1 Approach to Modeling

The watershed model involved coupling or linking three separate modules or minimodels: hydrodynamics, soil dynamics, and ecological productivity. The current version of the model is the latest in a long series of modifications to a model originally proposed over 20 years ago (Sklar et al., 1985; Costanza et al., 1990). The original model has been repeatedly updated as better ecological information has become available (Sklar et al., 2001; Martin et al., 2002; Reyes et al., 2004). The three modules perform their computations on each cell of a grid of cells (Fig. 21.7), and predicted values can be exchanged among neighboring cells.

The hydrodynamics module computed water levels and depth velocities and the transport of material (i.e., salt and sediments) among the grid cells using

(a)   1988 USF&WS

(b) 1988 Calibration
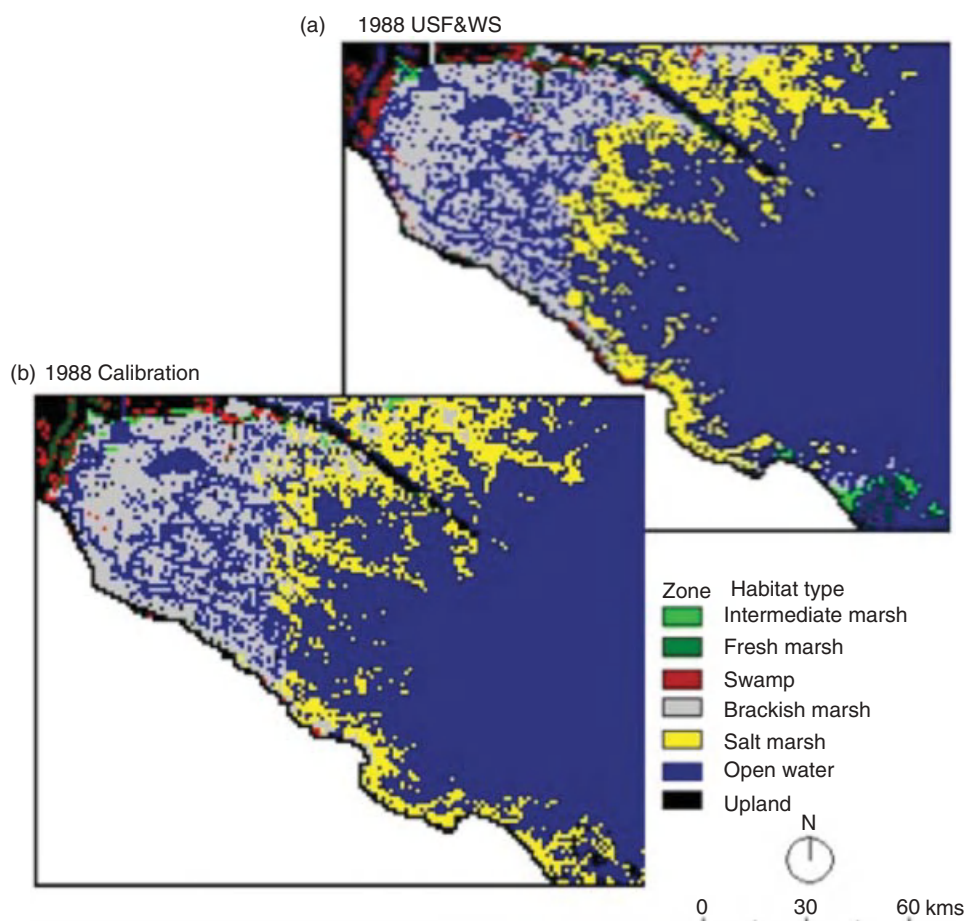
FIGURE 21.7   Habitat map for 1988 (a) estimated by the US Fish & Wildlife and (b) predicted by the watershed model.

what is technically called a two-dimensional, vertically averaged, finite difference approach (Singh and Aravamuthan, 1995). Basically, the hydrodynamics model simulates how water moves among the grid cells forced by tides, river discharge, and wind. The result is an updating of the water levels (including drying), water velocities, and flux of material for all cells in the grid every 12 min. In order to simulate water movement, the boundary conditions included fresh water input to the grid and the seasonal tidal height at the edge of the grid. These data were available from field measurements.

The soil dynamics module computed the build-up of land or the development of open water for each grid cell every day. The change in the amount of sediments in each cell was the balance between the input of sediments from other cells, local organic peat deposition creating sediments, loss of sediments because of erosion, and the lowering of the elevation of the cell because of subsidence. The net effect of the computed changes in sediments was the determination of the elevation of the land in each cell. This new

elevation, coupled with the hydrodynamic output, determined the water levels in a cell.

The productivity module calculated the net primary productivity for marsh and swamp plant communities on each grid cell every day. The ecological module computed the new values of biomass above ground and biomass below ground as a function of the present biomass, the maximum growth rate, and an environmental limiting function that accumulated daily information on temperature, water level, and salinity into a single monthly adjustment factor (Hopkinson et al., 1988; Mitsch, 1988; Nyman and DeLaune, 1991).

Every 2 years, each grid cell was assigned a habitat type. There were seven possible habitat types allowed: intermediate marsh, fresh marsh, swamp, brackish marsh, salt marsh, open water, and upland. Daily environmental conditions (amount of sediment deposited, hours of flooding, salinity) and the amount of biomass present were tracked over the two years. At the end of each second year, the tallied information was used to assign a habitat type and a map of

habitat types was obtained. For example, if more than half of the counts in the tally were open water, the cell was assigned as open water. This accumulated information was also used to update the elevation and other aspects of each cell, which was then sent to the hydrodynamic module to use for the next 2 years before being updated again.

21.5.2 Model Calibration

The watershed model applied to Caernarvon was calibrated and validated using a multiple resolution fit analysis (Costanza, 1989) that compared actual habitat maps of plant communities to the maps simulated by the watershed model (Reyes et al., 2000, 2003; Martin et al., 2002). The calibration was done by running the model for 10 years, using 1978 values as the starting values. The resulting map predicted for 1988 was then compared to the USFWS habitat map measured in 1988 (Fig. 21.7). These 10-year calibration runs were repeated, varying the initial spatial parameters (elevation) and forcing functions (boundary salinity and tidal elevations). A summary fit index (Costanza, 1989) was computed, and the calibration resulted in an index value of 94.1 out of a possible 100. The score of 94.1 was well above what is considered the acceptable validation standard for this type of model (Reyes et al., 2000, 2003; Martin et al., 2002).

21.5.3 Model Results

Before 2001, the Caernarvon diversion discharge regime was used to control salinity in the middle part of the basin by releasing low flows for long periods. Beginning in 2001, an experimental discharge (that we called *pulsed*) was implemented involving a high flow discharge followed by a no discharge for short periods. This high flow followed by no flow created a pulse in the fresh water input to the ecosystem. The calibrated model was used to predict the effects of different fresh water inputs on the long-term plant communities. The modeling results of three fresh water input scenarios are reported here. These scenarios were: no fresh water discharge (pre-1991 conditions), inclusion of a scheduled discharge (as that used to control salinity), and pulsed discharged (Day et al., 2003). The no discharge scenario meant that the diversion was not used to add water to the system, but water still entered via rain and other natural processes. The total amount of water delivered to the basin during the pulsed scenario is less than the total amount discharged during the scheduled discharge scenario. For the scheduled and pulsed scenarios, the pattern of water releases was repeated year after year for the 50 years of the simulation.

Two comparisons were made using the results of the simulations of the three scenarios. Both comparisons used the predicted map of the habitat types in each cell in the grid at the end of the 50-year simulations. The first comparison used the simulated results and compared them to the habitat map of the same area estimated for 1988. The total areas of the different habitat types (summed over the cells in year 50) for each of the three scenarios was compared to the total areas computed from the 1988 map. The second comparison involved comparing the spatial distributions of habitat types in year 50 from the scheduled and pulsed scenarios to the spatial distribution predicted under the no discharge scenario. Difference maps were used to spatially analyze where habitat changes would be predicted to occur (Fig. 21.8). A difference map was computed by comparing cell by cell the predicted habitat types between the no discharge and scheduled and between the no discharge and pulsed maps. When a cell changed from the open water under the no discharge map to brackish marsh under the other scenario, it was noted as blue, salt marsh to brackish marsh changes were noted in yellow, and brackish marsh to salt marsh were noted as light green.

Predicted total number of cells (or total area) of the different habitat types after 50 years under the three scenarios was quite similar (Table 21.2). Model results generally showed that adding fresh water, even the amounts under the no discharge scenario, had a beneficial effect on the marsh communities. All three scenarios resulted in more land habitat and less open water habitat than was estimated from the 1988 habitat map. Under the no discharge scenario, open water area was reduced by 31 km^2 compared to the 1988 map, with brackish marsh presenting the largest gains (482–562, or a gain of 80 km^2). The scheduled discharge scenario also resulted in a net gain of land compared to the 1988 map, but showed more increase in brackish marsh and less increase in salt marsh than was predicted under the no discharge scenario. The pulsed scenario resulted in very similar changes in habitat areas as the no discharge scenario.

The difference maps showed that while the total amount of habitat change was similar among the three scenarios, there were some spatial differences in where these habitat changes occurred (Fig. 21.8). In particular, the scheduled discharge scenario differed from the no discharge scenario in predicting brackish marsh rather than salt marsh (yellow) in the central portion of the watershed and salt marsh rather than brackish marsh (light green) in the northern portion

No discharge 2037

Normal discharge 2037

Pulses discharge 2037

Difference no discharge - normal discharge

Difference no discharge - pulses discharge
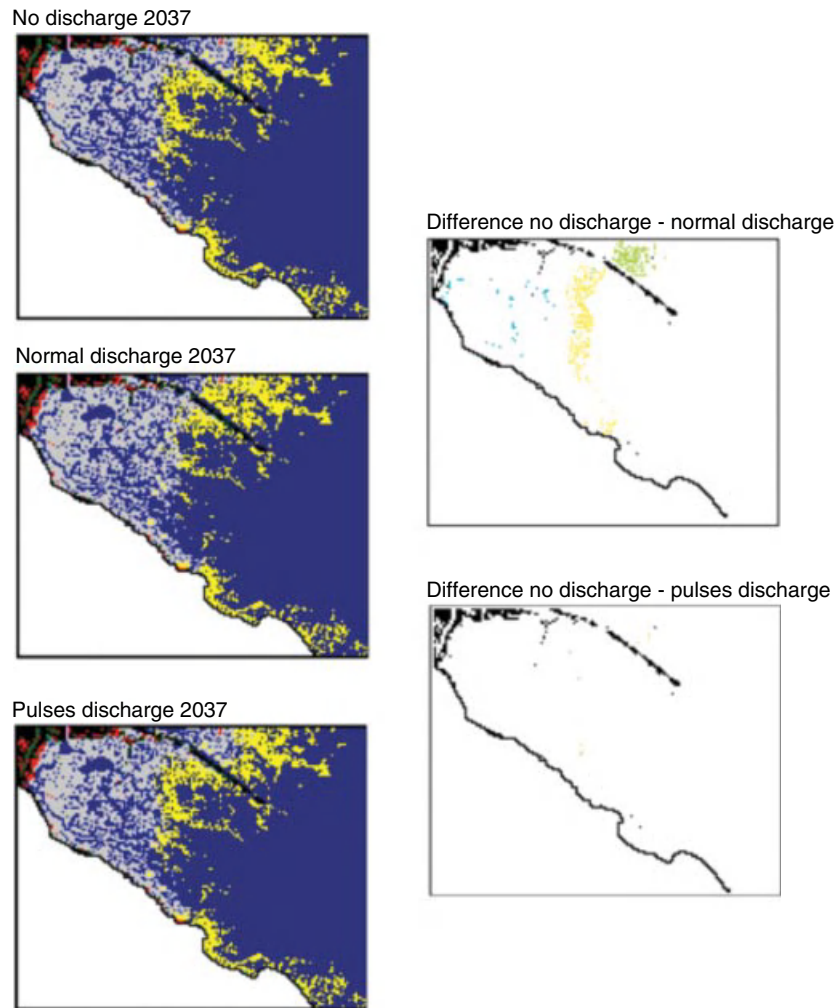
FIGURE 21.8 Predicted habitat maps for the no discharge, scheduled releases, and pulsed releases scenarios for year 50 of model simulations. Also shown are the difference maps that compare cell by cell the predicted habitat map under no discharge in year 50 to the map under the scheduled scenario in year 50 and the no discharge to the pulsed scenario. The colors on the difference maps indicate the type of habitat changes that were predicted: open water to brackish marsh (blue), salt marsh to brackish marsh (yellow), and brackish to salt marsh (light green).

TABLE 21.2 Comparison of habitat extension for future conditions (2037) under three different discharge regimes

Habitat type	Habitat Extension (km²)			
	1988 USFWS Map	No Discharge	Scheduled Discharge	Pulsed Discharge
Intermediate marsh	16	2	2	2
Fresh marsh	60	34	34	34
Swamp	43	32	32	32
Brackish marsh	482	562	601	562
Salt marsh	359	362	333	361
Open water	2444	2413	2403	2413

of the watershed. When compared to the other two scenarios, the scheduled discharge scenario resulted in the most favorable conditions to preserve the spatial distribution of habitats and prevent further land loss.

21.5.4 Lessons Learned

The present watershed model provided a quantitative way to predict the large-scale and long-term effects of pulses of water on the plant community. The model

results illustrated how the timing and magnitude of water delivery can affect the spatial changes in habitat types while still resulting in similar total amounts of various habitat types. The modeling results also confirmed the capability of the diversion to maintain salinity downstream in the watershed, thereby reducing any further extension inland of the salt marsh habitat. Further testing of the pulsed discharge using the model is needed. Data used for the pulsed scenario was from only 2 years of data collection. But even with this limited information, the model results question the timing of the pulsed discharge that has been used to date. The pulse discharges so far were done during the late winter to early spring period. Further simulations could contribute to evaluate the potential of delivering the pulses of water during the marsh growing season. Modeling of the effects of pulsed water releases must proceed with some caution, because potential negative effects, such as flood stress to the wetlands and increased algal blooms (Day et al., 1995), are not explicitly considered in the model. Watershed simulation models, such as the one described here, offer a powerful tool for evaluating the cumulative effects of changes arising from global warming, cumulative impacts, and future human development, and for evaluating the potential for the success of diverse management strategies (Reyes et al., 1996, 2003; DeAngelis et al., 1998; Rybczyk et al., 1998; Sklar and Browder, 1998).

21.6 THE FUTURE

The use of estuarine modeling is accelerating as our knowledge about estuarine ecosystems expands, computing power continues to increase, and the questions and issues of interest become ever more complex. We briefly described estuarine modeling in this chapter and outlined a series of steps involved in most model applications. The three case studies illustrated how models are constructed, the diverse mathematics that are used to express models, and the power of modeling in addressing important environmental issues. We barely discussed the management applications of estuarine models. For example, population dynamics models are relied on for setting annual harvesting quota for many fish and shellfish species in coastal areas (Rose and Cowan, 2003). We are optimistic that continued effort in modeling will lead to improved understanding of estuarine ecosystems, more informative field and laboratory data, and better informed management decisions. This is a challenge that must be met as environmental problems become more complex and we recognize more and more that the physics, chemistry, and biology of estuaries are highly coupled.

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